CHAPTER 1

Veterinary helminthology

PRINCIPLES OF CLASSIFICATION

When examined, living organisms can be seen to form natural groups with features in common. These similarities may be morphological, but increasingly may be based on DNA analysis. Groups of organisms are combined into biologically meaningful groups, usually attempting to represent evolutionary pathways. A group of this sort is called a **taxon** and the study of this aspect of biology is called **taxonomy**. The study of the complex systems of interrelationship between living organisms is called **systematics**. The taxa into which organisms may be placed are recognised by international agreement; the primary ones are **kingdom**, **phylum**, **class**, **order**, **family**, **genus** and **species**. The intervals between these are large, and some organisms cannot be allocated to them precisely, so intermediate taxa, prefixed appropriately, have been formed; examples of these are the **suborder** and the **superfamily**. As an example, the taxonomic status of one of the common abomasal parasites of ruminants may be expressed as shown below.

Kingdom	Animalia
Phylum	Nematoda
Class	Chromadorea
Order	Rhabditida
Suborder	Rhabditina
Superfamily	Trichostrongyloidea
Family	Trichostrongylidae
Subfamily	Haemonchinae
Genus	*Haemonchus*
Species	*contortus*

The names of taxa must follow a set of internationally agreed rules, but it is permissible to anglicise the endings, so that members of the superfamily Trichostrongyloidea in the example above may also be termed trichostrongiloids. The names of the genus and species are expressed in Latin form, the generic name having a capital letter, and they must be in grammatical agreement. It is customary to print Latin names in italics. Accents are not permitted. If an organism is named after a person, amendment may be necessary; the name of Müller, for example, has been altered in the genus *Muellerius*.

HELMINTHOLOGY

Parasitic helminths can affect humans, animals and plants, with estimated numbers of between 75 000 and 300 000 species. The higher taxa containing helminths of veterinary importance are as follows.

Major
- Nematoda (roundworms)
- Platyhelminthes (flatworms)
  - Trematoda (flukes)
  - Cestoda (tapeworms)

Minor
- Acanthocephala (thorny-headed worms)

PHYLUM NEMATODA

The nematodes (Nematoda) are commonly called **Roundworms** from their appearance in cross-section, and are parasitic or free-living. In the majority of nematodes the sexes are separate.

CLASSES CHROMADOREA AND ENOPLEA

The system of classification of nematodes of veterinary importance, which is based on current taxonomic literature, is given in taxonomic tables. In this system, nematode genera and species are divided in the classes Chromadorea and Enoplea, which are grouped into several **superfamilies**. The superfamilies can be conveniently divided into **bursate** and **non-bursate** groups, the most typical features of which are summarised in Table 1.1.

STRUCTURE AND FUNCTION

Most nematodes have a cylindrical unsegmented form, tapering at either end, and the body is covered by a colourless, somewhat translucent, layer: the cuticle. The tough **cuticle** is secreted by the underlying **hypodermis**, which projects into the body cavity forming two **lateral cords,** which carry the excretory canals, and a dorsal and ventral cord carrying the **nerves** (Fig. 1.1). The muscle cells, arranged longitudinally, lie between the hypodermis and the body cavity. The latter contains fluid at a high pressure, which maintains the turgidity and shape of the body (pseudocoelom). Locomotion is effected by undulating waves of muscle contraction and relaxation that alternate on the dorsal and ventral aspects of the worm. A circular muscle layer is absent in nematodes. Most of the internal organs are filamentous and suspended in the fluid-filled body cavity (Fig. 1.1). The **digestive system** is tubular (Fig. 1.2a). The mouth, or stoma, of many nematodes is a simple opening, which may be

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Table 1.1 Characteristic features of parasitic nematodes of veterinary importance.

Superfamily	Typical features
Bursate nematodes	
Trichostrongyloidea *Trichostrongylus*, *Ostertagia*, *Dictyocaulus*, *Haemonchus*, etc.	Buccal capsule small. Life cycle **direct**; infection by L_3
Strongyloidea *Strongylus*, *Syngamus*, etc.	Buccal capsule well developed; leaf crowns and teeth usually present. Life cycle **direct**; infection by L_3
Ancylostomatoidea *Ancylostoma*, *Uncinaria*, etc.	
Metastrongyloidea *Metastrongylus*, *Muellerius*, *Protostrongylus*, etc.	Buccal capsule small. Life cycle **indirect**; infection by L_3 in intermediate host
Non-bursate nematodes	
Rhabditoidea *Strongyloides*, *Rhabditis*, etc.	Very small worms; buccal capsule small. Free-living and parasitic generations. Life cycle **direct**; infection by L_3
Ascaridoidea *Ascaris*, *Toxocara*, *Parascaris*, etc.	Large white worms. Life cycle **direct**; infection by L_2 in egg
Dioctophymatoidea *Dioctophyma*, etc.	Very large worms. Life cycle **indirect**; infection by L_3 in aquatic annelids
Oxyuroidea *Oxyuris*, *Skrjabinema*, etc.	Female has long pointed tail. Life cycle **direct**; infection by L_3 in egg
Spiruroidea *Spirocerca*, *Habronema*, *Thelazia*, etc.	Spiral tail in male. Life cycle **indirect**; infection by L_3 from insects
Filarioidea *Dirofilaria*, *Onchocerca*, *Parafilaria*, etc.	Long thin worms. Life cycle **indirect**; infection by L_3 from insects
Trichuroidea *Trichuris*, *Capillaria*	Whip-like or hair-like worms. Life cycle **direct** or **indirect**; infection by L_1
Trichinelloidea *Trichinella*, etc.	

surrounded by two or three lips, and leads directly into the oesophagus. Where the mouth opening is large and well developed it is often surrounded by a leaf crown. In others, such as the strongyloids, it is large, and opens into a **buccal capsule**, which may contain blades or teeth. Such parasites, when feeding, draw a plug of mucosa into the buccal capsule, where it is broken down by the action of enzymes, which are secreted into the capsule from adjacent glands. Some of these worms may also secrete anticoagulant, and small vessels, ruptured in the digestion of the mucosal plug, may continue to bleed for some minutes after the worm has moved to a fresh site.

Those nematodes with very small buccal capsules, like the trichostrongyloids, or simple oral openings, like the ascaridoids, generally feed on mucosal fluid, products of host digestion and cell debris, while others, such as the oxyuroids, appear to scavenge on

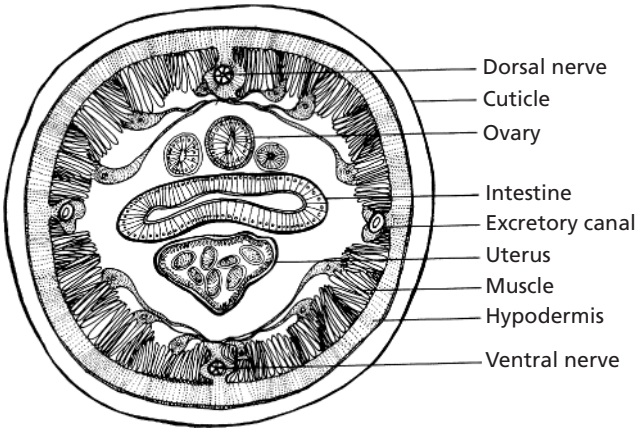


Fig. 1.1 Transverse section of a generalised female nematode.

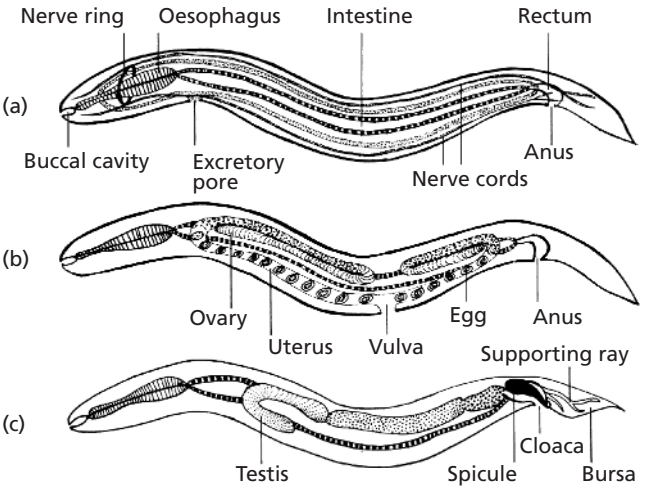


Fig. 1.2 Longitudinal sections of a generalised nematode. (a) Digestive, excretory and nervous system. (b) Reproductive system of a female nematode. (c) Reproductive system of a male nematode.

the contents of the lower gut. Worms living in the bloodstream or tissue spaces, such as the filarioids, feed exclusively on body fluids. The **oesophagus** is usually muscular and pumps food into the intestine. It is of variable form (Fig. 1.3) and is a useful preliminary identification character for groups of worms. It may be **filariform**, simple and slightly thickened posteriorly, as in the bursate nematodes; **bulb shaped**, with a large posterior swelling, as in the ascaridoids; or **double bulb shaped**, as in the oxyuroids. In some

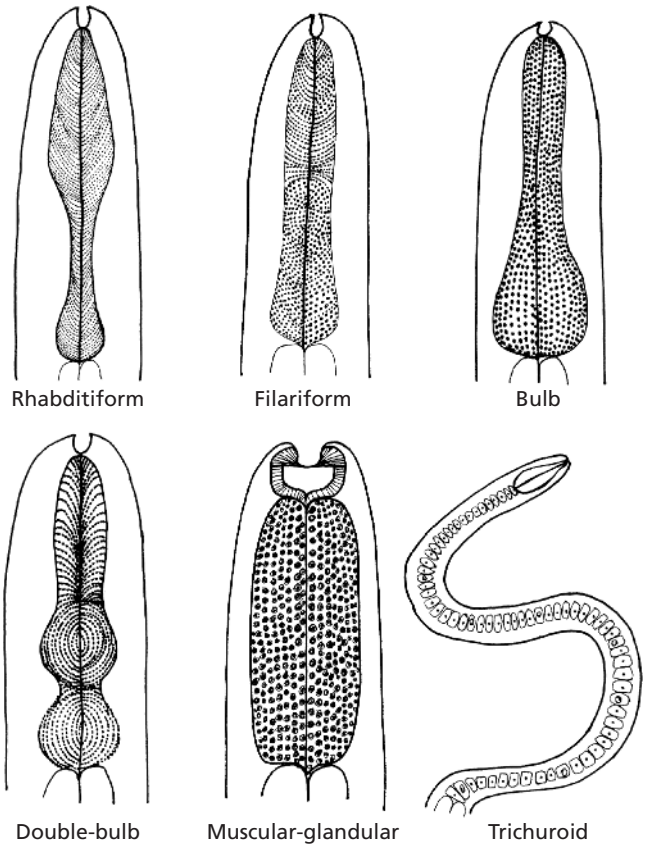


Fig. 1.3 The basic forms of oesophagus found in nematodes.

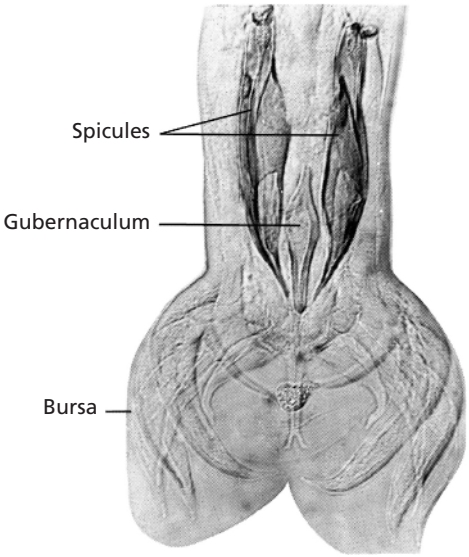


Fig. 1.4 Male trichostrongiloid nematode bursa showing spicules and bursa.

groups this wholly muscular form does not occur: the filarioids and spiruroids have a **muscular–glandular** oesophagus which is muscular anteriorly, the posterior part being glandular; the **trichuroid** oesophagus has a capillary form, passing through a single column of cells, the whole being known as a stichosome. A **rhabditiform** oesophagus, with slight anterior and posterior swellings, is present in the preparasitic larvae of many nematodes, and in adult free-living nematodes.

The **intestine** is a simple tube descending from the oesophagus whose lumen is enclosed by a single layer of epithelial cells or by a syncytium. The luminal surfaces possess microvilli, which increase the absorptive capacity of the cells. In female worms the intestine terminates in an anus, while in males there is a cloaca which functions as an anus, into which opens the vas deferens and through which the copulatory spicules may be extruded.

The so-called '**excretory system**' is very primitive, consisting of a canal within each lateral cord joining at the excretory pore in the oesophageal region. The **reproductive systems** consist of filamentous tubes, which float in the body cavity. The **female organs** comprise ovary, oviduct and uterus, which may be paired (didelphic) or sometimes single (monodelphic), ending in a common short vagina, which opens at the vulva (Fig. 1.2b). The location of the vulva can be a useful aid in diagnosis, being at the anterior end (opisthodelphic), middle (amphidelphic) or posterior end (prodelphic). At the junction of uterus and vagina in some species, there is a short muscular organ, the ovejector, which regulates and assists in egg laying. A vulval flap may also be present. Nematodes can be oviparous, ovoviviparous or viviparous. The **male organs** consist of a single continuous testis and a vas deferens terminating in a muscular ejaculatory duct into the cloaca (Fig. 1.2c). Accessory male organs are sometimes important in identification, especially of the trichostrongyloids, the two most important being the spicules and gubernaculum (Fig. 1.4). The **spicules** are chitinous organs, usually paired, which are inserted in the female genital opening during copulation. In some species they are absent (e.g. *Trichinella*) or only one spicule is present (e.g. *Trichuris*). The **gubernaculum**, also chitinous, is a small structure located in the dorsal wall, which acts as a guide for the spicules. When the guide is located in the ventral wall it is referred to as a **telamon**. With the two sexes in close apposition, the amoeboid sperm are transferred from the cloaca of the male into the uterus of the female. The **cuticle** may be modified to form various structures (Fig. 1.5), the more important of which include the following.

- **Leaf crowns** consisting of rows of papillae occurring as fringes round the rim of the buccal capsule (external leaf crowns) or just inside the rim (internal leaf crowns). They are especially prominent in certain nematodes of horses. Their function is not known, but it is suggested that they may be used to pin a patch of mucosa in position during feeding, or that they may prevent the entry of foreign matter into the buccal capsule when the worm has detached from the mucosa.
- **Cervical papillae** occur anteriorly in the oesophageal region, and **caudal papillae** posteriorly at the tail. They are spine-like or finger-like processes, and are usually diametrically placed. Their function may be sensory or supportive.
- **Cervical** and **caudal alae** are flattened wing-like expansions of the cuticle in the oesophageal and tail regions respectively.

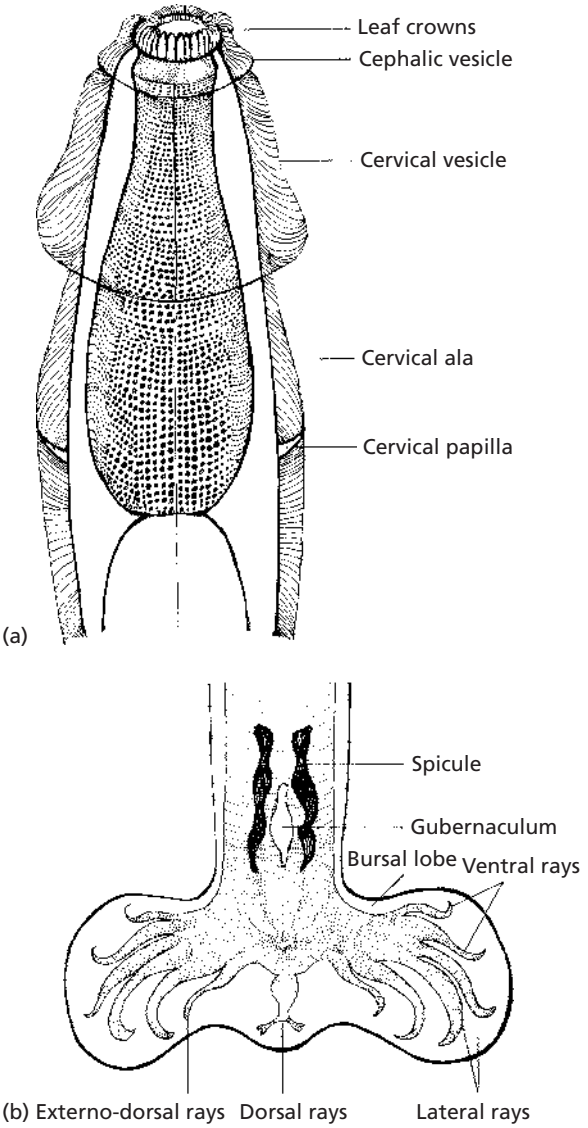


Fig. 1.5 Cuticular modifications of a generalised nematode: (a) anterior region; (b) posterior region of a male.

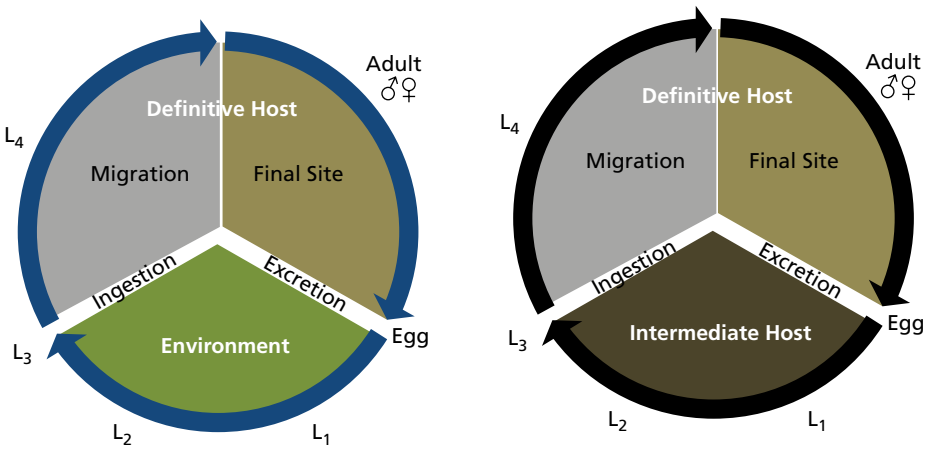


Fig. 1.6 Generalised nematode life cycles: (a) direct; (b) indirect.

- **Cephalic** and **cervical vesicles** are inflations of the cuticle around the mouth opening and in the oesophageal region.
- The **copulatory bursa**, which embraces the female during copulation, is important in the identification of certain male nematodes and is derived from much expanded caudal alae, which are supported by elongated caudal papillae called **bursal rays**. It consists of two lateral lobes and a single small dorsal lobe. It is particularly well developed in the strongylids.
- **Plaques** and **cordons** are plate-like and cord-like ornamentations present on the cuticle of many nematodes of the superfamily Spiruroidea.

BASIC NEMATODE LIFE CYCLE

In the Nematoda, the sexes are separate and the males are generally smaller than the females, which lay eggs or larvae. During development, a nematode moults at intervals, shedding its cuticle. In the complete life cycle there are four moults, the successive larval stages being designated L_1, L_2, L_3, L_4 and finally L_5, which is the immature adult.

One feature of the basic nematode life cycle is that immediate transfer of infection from one **final host** to another rarely occurs. Some development usually takes place either in the faecal pat or in a different species of animal, the **intermediate host**, before infection can take place.

In the common form of **direct** life cycle (Fig. 1.6a), the free-living larvae undergo two moults after hatching and infection is by ingestion of the free L_3 stage. There are some important exceptions, however, infection sometimes being by larval penetration of the skin or by ingestion of the egg containing a larva. In **indirect** life cycles (Fig. 1.6b), the first two moults usually take place in an intermediate host and infection of the final host is either by ingestion of the intermediate host or by inoculation of the L_3 when the intermediate host, such as a blood-sucking insect, feeds.

After infection, two further moults take place to produce the L_5 or immature adult parasite.

Following copulation, a further life cycle is initiated. In the case of gastrointestinal parasites, development may take place entirely in the gut lumen or with only limited movement into the mucosa. However, in many species, the larvae travel considerable distances through the body before settling in their final (predilection) site and this is the migratory form of life cycle. One of the most common routes is the **hepatic–tracheal**. This takes developing stages from the **gut** via the portal system to the **liver** then via the hepatic vein and posterior vena cava to the **heart** and from there via the pulmonary artery to the **lungs**. Larvae then travel via the bronchi, trachea and oesophagus to the **gut**. It should be emphasised that the above is a basic description of nematode life cycles and that there are many variations.

DEVELOPMENT OF THE PARASITE

Egg

Nematode eggs differ greatly in size and shape, and the shell is of variable thickness, usually consisting of three layers. The inner membrane, which is thin, has lipid characteristics and is impermeable. A middle layer, which is tough and chitinous, gives rigidity and, when thick, imparts a yellowish colour to the egg. In many species this layer is interrupted at one or both ends with an operculum (lid) or plug. The third outer layer consists of protein, which is very thick and sticky in the ascaridoids and is important in the epidemiology of this superfamily. In contrast, in some species the eggshell is very thin and may be merely present as a sheath around the larva. The survival potential of the egg outside the body varies, but appears to be connected with the thickness of the shell, which protects the larva from desiccation. Thus parasites whose infective form is the larvated egg usually have very thick-shelled eggs which can survive for years on the ground.

Hatching

Depending on the species, eggs may hatch outside the body or after ingestion. Outside the body, hatching is controlled partly by factors such as temperature and moisture and partly by the larva itself. In the process of hatching, the inner impermeable shell membrane is broken down by enzymes secreted by the larva and by its own movement. The larva is then able to take up water from the environment and enlarges to rupture the remaining layers and escape.

When the larvated egg is the infective form, the host initiates hatching after ingestion by providing stimuli for the larva, which then completes the process. It is important for each nematode species that hatching should occur in appropriate regions of the gut and hence the stimuli will differ, although it appears that dissolved carbon dioxide is a constant essential.

Larval development and survival

Three of the important superfamilies, the trichostrongyloids, the strongyloids and the rhabditoids, have a completely free-living preparasitic phase. The first two larval stages usually feed on bacteria but the L_3, sealed off from the environment by the retained cuticle of the L_2, cannot feed and must survive on the stored nutrients acquired in the early stages. Growth of the larva is interrupted during moulting by periods of lethargus in which it neither feeds nor moves.

The cuticle of the L_2 is retained as a sheath around the L_3; this is important in larval survival with a protective role analogous to that of the eggshell in egg-infective groups. The two most important components of the external environment are temperature and humidity. The optimal temperature for the development of the maximum number of larvae in the shortest feasible time is generally in the range 18–26 °C. At higher temperatures, development is faster and the larvae are hyperactive, thus depleting their lipid reserves. The mortality rate then rises, so that few will survive to L_3. As the temperature falls, the process slows and below 10 °C, the development from egg to L_3 usually cannot take place. Below 5 °C movement metabolism of L_3 is minimal, which in many species favours survival.

The optimal humidity is 100%, although some development can occur down to 80% relative humidity. It should be noted that even in dry weather where the ambient humidity is low, the microclimate in faeces or at the soil surface may be sufficiently humid to permit continuing larval development.

In the trichostrongyloids and strongyloids, the embryonated egg and the ensheathed L_3 are best equipped to survive in adverse conditions such as freezing or desiccation; in contrast, the L_1 and L_2 are particularly vulnerable. Although desiccation is generally considered to be the most lethal influence in larval survival, there is increasing evidence that by entering a state of anhydrobiosis, certain larvae can survive severe desiccation.

On the ground most larvae are active, although they require a film of water for movement and are stimulated by light and temperature. It is now thought that larval movement is mostly random and encounter with grass blades accidental.

Infection

As noted previously, infection may be by ingestion of the free-living L_3, and this occurs in the majority of trichostrongyloid and strongyloid nematodes. In these, the L_3 sheds the retained sheath of the L_2 within the alimentary tract of the host, the stimulus for exsheathment being provided by the host in a manner similar to the hatching stimulus required by egg-infective nematodes. In response to this stimulus the larva releases its own exsheathing fluid, containing an enzyme, leucine aminopeptidase, which dissolves the sheath from within, either at a narrow collar anteriorly, so that a cap detaches, or by splitting the sheath longitudinally. The larva can then wriggle free of the sheath.

As in the preparasitic stage, growth of the larva during parasitic development is interrupted by two moults, each of these occurring during a short period of lethargus. The time taken for development from infection until mature adult parasites are producing eggs or larvae is known as the **prepatent period** and this is of known duration for each nematode species.

METABOLISM

The main food reserve of preparasitic nematode larvae, whether inside the eggshell or free-living, is lipid, which may be seen as droplets in the lumen of the intestine. The infectivity of these stages is often related to the amount of lipid present; larvae which have depleted their reserves are not as infective as those which still retain quantities of lipid.

Apart from these reserves, the free-living first- and second-stage larvae of most nematodes feed on bacteria. However, once they reach the infective third stage, they are sealed in the retained cuticle of the second stage, cannot feed and are completely dependent on their stored reserves.

In contrast, the adult parasite stores its energy as glycogen, mainly in the lateral cords and muscles, and this may constitute 20% of the dry weight of the worm.

Free-living and developing stages of nematodes usually have an aerobic metabolism, whereas adult nematodes can metabolise carbohydrate by both glycolysis (anaerobic) and oxidative decarboxylation (aerobic). However, in the latter, pathways may operate which are not present in the host and it is at this level that some antiparasitic drugs operate.

The oxidation of carbohydrates requires the presence of an electron transport system, which in most nematodes can operate aerobically down to oxygen tensions of 5 mmHg or less. Since the oxygen tension at the mucosal surface of the intestine is around 20 mmHg, nematodes in close proximity to the mucosa normally have sufficient oxygen for aerobic metabolism. Otherwise, if the nematode is temporarily or permanently some distance from the mucosal surface, energy metabolism is probably largely anaerobic.

As well as the conventional cytochrome and flavoprotein electron transport system, many nematodes have 'haemoglobin' in their body fluids which gives them a red pigmentation. This nematode haemoglobin is chemically similar to myoglobin and has the highest affinity for oxygen of any known animal haemoglobin. The main function of nematode haemoglobin is thought to be to transport oxygen, acquired by diffusion through the cuticle or gut, into the tissues; blood-sucking worms presumably ingest a considerable amount of oxygenated nutrients in their diet.

The end products of the metabolism of carbohydrates, fats or proteins are excreted through the anus or cloaca, or by diffusion through the body wall. Ammonia, the terminal product of protein metabolism, must be excreted rapidly and diluted to non-toxic levels in the surrounding fluids. During periods of anaerobic carbohydrate metabolism, the worms may also excrete pyruvic acid rather than retaining it for future oxidation when aerobic metabolism is possible.

The 'excretory system' terminating in the excretory pore is almost certainly not concerned with excretion, but rather with osmoregulation and salt balance.

Two phenomena which affect the normal parasitic life cycle of nematodes and which are of considerable biological and epidemiological importance are arrested larval development and the periparturient rise in faecal egg counts.

ARRESTED LARVAL DEVELOPMENT

(Synonyms: inhibited larval development, hypobiosis)
This phenomenon may be defined as the temporary cessation in development of a nematode at a precise point in its parasitic development. It is usually a facultative characteristic and affects only a proportion of the worm population. Some strains of nematodes have a high propensity for arrested development while in others this is low. The stage at which larvae become arrested varies between species of nematodes; for example, L_3 stage in *Trichostrongylus*, Cyathostominae and *Ancylostoma*, L_4 stage in *Ostertagia*, *Teladorsagia*, *Haemonchus* and *Obeliscoides*, or immature adults as in *Dictyocaulus*.

Conclusive evidence for the occurrence of arrested larval development can only be obtained by examination of the worm population in the host. It is usually recognised by the presence of large numbers of larvae at the same stage of development in animals withheld from infection for a period longer than that required to reach that particular larval stage.

The nature of the stimulus for arrested development and for the subsequent maturation of the larvae is still a matter of debate. Although there are apparently different circumstances which initiate arrested larval development, most commonly the stimulus is an environmental one received by the free-living infective stages prior to ingestion by the host. It may be seen as a ruse by the parasite to avoid adverse climatic conditions for its progeny by remaining sexually immature in the host until more favourable conditions return. The name commonly applied to this seasonal arrestment is **hypobiosis**. Thus, the accumulation of arrested larvae often coincides with the onset of cold autumn/winter conditions in the northern hemisphere or very dry conditions in the subtropics or tropics. In contrast, the maturation of these larvae coincides with the return of environmental conditions suitable to their free-living development, although it is not clear what triggers the signal to mature and how it is transmitted.

The degree of adaptation to these seasonal stimuli and therefore the proportion of larvae which do become arrested seem to be heritable traits and are affected by various factors, including grazing systems and the degree of adversity in the environment. For example, in Canada where the winters are severe, most trichostrongyloid larvae ingested in late autumn or winter become arrested, whereas in southern Britain with moderate winters, about 50–60% are arrested. In the humid tropics where free-living larval development is possible all the year round, relatively few larvae become arrested.

However, arrested development may also occur as a result of both acquired and age immunity in the host and although the proportions of larvae arrested are not usually so high as in hypobiosis, they can play an important part in the epidemiology of nematode infections. Maturation of these arrested larvae seems to be linked with the breeding cycle of the host and occurs at or around parturition.

The epidemiological importance of arrested larval development from whatever cause is that, first, it ensures the survival of the nematode during periods of adversity and, second, the subsequent maturation of arrested larvae increases the contamination of the environment and can sometimes result in clinical disease.

PERIPARTURIENT RISE IN FAECAL EGG COUNTS

(Synonyms: postparturient rise, spring rise)
Periparturient rise (PPR) refers to an increase in the numbers of nematode eggs in the faeces of animals around parturition. This phenomenon is most marked in ewes, goats and sows and recent data support the hypothesis that there is competition for nutrients between the immune system, the rapidly growing fetus in late pregnancy and the udder during lactation, particularly metabolisable protein. This relaxation of immunity can be largely restored by supplementation with rumen-undegradable protein and is also influenced by the body protein status of the ewe.

The source of the PPR is threefold.

1. Maturation of larvae arrested due to host immunity.
2. An increased establishment of infections acquired from the pastures and a reduced turnover of existing adult infections.
3. An increased fecundity of existing adult worm populations.

Contemporaneously, but not associated with the relaxation of host immunity, the PPR may be augmented by the maturation of hypobiotic larvae.

The importance of the PPR is that it occurs at a time when the numbers of new susceptible hosts are increasing and so ensures the survival and propagation of the worm species. Depending on the magnitude of infection, it may also cause a loss of production in lactating animals and, by contamination of the environment, lead to clinical disease in susceptible young stock.

NEMATODE SUPERFAMILIES

SUPERFAMILY TRICHOSTRONGYLOIDEA

In some recent taxonomic classification, this superfamily is included within the superfamily Strongyloidea. The trichostrongyloids are small, often hair-like, worms in the bursate group, which, with the exception of the lungworm *Dictyocaulus*, parasitise the alimentary tract of animals and birds. Structurally, they have few cuticular appendages and the buccal capsule is vestigial and possesses no leaf crowns. Teeth are usually absent. The males have a well-developed bursa with large lateral lobes and two spicules, the configuration of which is used for species differentiation. The life cycle is direct and usually non-migratory and the ensheathed L_3 is the infective stage. The trichostrongiloids are responsible for considerable mortality and widespread morbidity, especially in ruminants.

The most important alimentary genera are *Ostertagia*, *Haemonchus*, *Trichostrongylus*, *Cooperia*, *Nematodirus*, *Hyostrongylus*, *Marshallagia* and *Mecistocirrus*. *Dictyocaulus* is an important genus affecting the respiratory tract of ruminants and horses. Other genera of lesser importance are *Graphidium*, *Obeliscoides*, *Ollulanus*, *Libyostrongylus*, *Graphinema*, *Impalaia*, *Ornithostrongylus*, *Amidostomum*, *Epomidiostomum*, *Nematodirella*, *Lamanema*, *Nippostrongylus* and *Nematospiroides*.

FAMILY TRICHOSTRONGYLIDAE

Trichostrongylus

Adult worms are small, slightly reddish/brown in colour, slender and hair-like, usually less than 7 mm long (Fig. 1.7) and difficult to see with the naked eye. The worms have no obvious buccal capsule and cephalic inflations are absent. A most useful generic character is the distinct excretory notch in the oesophageal region (Fig. 1.8). The male bursa has long lateral lobes, while the dorsal lobe is not well defined with a slender dorsal ray, which is cleft near its tip into two branches. The ventro-ventral ray is well separated from the other rays. The spicules are thick and unbranched and a gubernaculum is present. Species identification is based on the shape and size of the spicules (Tables 1.2 and 1.3). In the female,

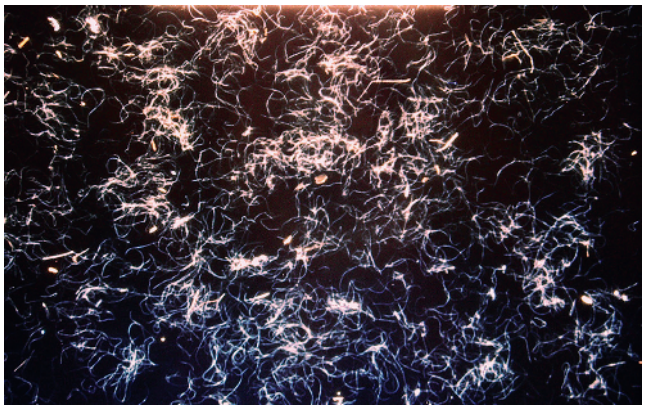


Fig. 1.7 Adult *Trichostrongylus* worms.

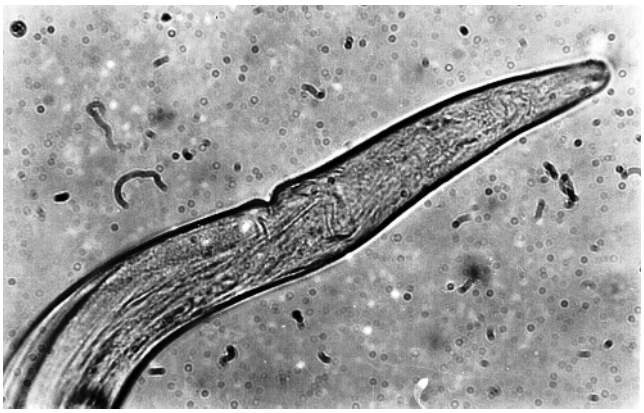


Fig. 1.8 Characteristic excretory notch in the oesophageal region of *Trichostrongylus*.

the tail is bluntly tapered (Fig. 1.9) and there is no vulval flap and the vulva opens a short distance from the middle of the body. The females possess double ovejectors.

Life cycle: This is direct and the preparasitic phase is typically trichostrongyloid, eggs developing to the infective L_3 in about 7–10 days under optimal conditions. Following ingestion and exsheathment, larvae penetrate the mucosa of the small intestine (Fig. 1.10) and after two moults the fifth-stage worms are present under the intestinal epithelium around two weeks after initial infection. The prepatent period is generally 2–3 weeks.

Table 1.2 Identification of *Trichostrongylus* spp. based on male spicule morphology.

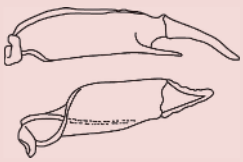
Species	Spicules: description	Spicules: morphology
Trichostrongylus axei	Spicules are dissimilar and unequal in length (the right being shorter than the left)	(a) 
Trichostrongylus colubriformis	Thick, brown, unbranched, of equal length and terminate in a barb-like tip	(b) 
Trichostrongylus vitrinus	Thick, unbranched, of equal length and end in a point	(c) 
Trichostrongylus longispicularis	The spicules are stout, brown, unbranched, slightly unequal in length and terminate in a tapering blunt tip that has a small semi-transparent protrusion	(d) 
Trichostrongylus rugatus	Spicules are unequal and dissimilar, bearing transverse ridges near the tip	(e) 
Trichostrongylus falculatus	Spicules subequal – 100 µm long	(f) 
Trichostrongylus capricola	Spicules are equal in length. Thinner distally than anteriorly and terminate in a rounded tip	(g) 
Trichostrongylus retortaeformis	Spicules are stout, unequal in length and terminate in a barb-like tip	(h) 

Table 1.3 *Trichostrongylus* species.

Species	Hosts	Site
Trichostrongylus axei (syn. *Trichostrongylus extenuatus*)	Cattle, sheep, goats, deer, horses, pigs	Abomasum or stomach
Trichostrongylus colubriformis	Cattle, sheep, goats, camels, rabbits, pigs, dogs, humans	Duodenum, anterior small intestine
Trichostrongylus vitrinus	Sheep, goats, camels, deer, rabbits	Duodenum, small intestine
Trichostrongylus capricola	Sheep, goats	Small intestine
Trichostrongylus falculatus	Sheep, goats, antelopes	Small intestine
Trichostrongylus longispicularis	Sheep, cattle, goats, camels, deer, llamas	Small intestine
Trichostrongylus probolurus	Sheep, goats, camels, occasionally humans	Stomach, small intestine
Trichostrongylus rugatus	Sheep, goats	Small intestine
Trichostrongylus retortaeformis	Rabbits, hares	Small intestine
Trichostrongylus calcaratus	Rabbits, hares	Small intestine
Trichostrongylus affinus	Rabbits, sheep, occasionally humans	Small intestine
Trichostrongylus tenuis	Gamebirds (grouse, partridges, pheasants), chickens, ducks, geese, turkeys, emus	Small intestine, caecae

Fig. 1.9 Tail of adult female *Trichostrongylus*.

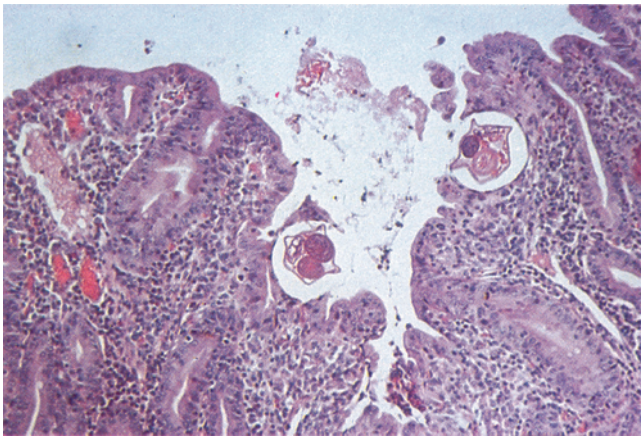


Fig. 1.10 Developing *Trichostrongylus vitrinus* in the small intestinal mucosa.

Trichostrongylus axei

Synonym: *Trichostrongylus extenuatus*

Common name: Stomach hairworm

Description, gross: The adults are small, hair-like, light brownish-red and difficult to see with the naked eye. Males measure around 3–6 mm and females 4–8 mm in length. There is no buccal capsule and the anterior of the worm and the vulval area lack any accessory cuticular structures. The bursa is simple in form and the ventro-ventral ray is positioned well apart from the other rays. The male spicules are dissimilar and unequal in length, the right being shorter than the left (Fig. 1.11; Table 1.2a). The female has double ovejectors. The eggs are medium-sized, an irregular ellipse and measure about 70–106 by 30–45 µm. The poles are dissimilar, one being more rounded, and are not very wide (see Fig. 4.4).

Trichostrongylus colubriformis

Synonym: *Trichostrongylus instabilis*

Common name: Black scour or bankrupt worm

Description: Males measure around 4–5.5 mm and females 5.5–7.5 mm in length. There is no buccal capsule and the anterior of the worm and the vulval area lack any accessory cuticular structures. The bursa is simple in form and the ventro-ventral ray is positioned well apart from the other rays. The spicules are thick, brown, unbranched, of equal length and terminate in a barb-like tip (Fig. 1.12; Table 1.2b). The female has double ovejectors. The thin-shelled eggs are medium-sized, an irregular ellipse and measure about 79–101 by 38–50 µm. The poles are dissimilar, one being more rounded, and are not very wide. The eggs are segmenting when laid.

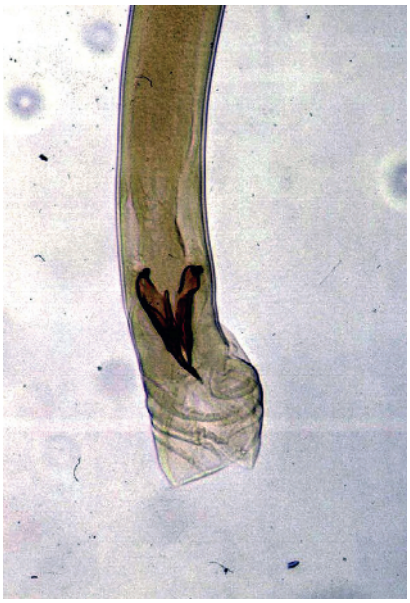


Fig. 1.11 Copulatory bursa and spicule of *Trichostrongylus axei*.

Fig. 1.12 Copulatory bursa and spicule of *Trichostrongylus colubriformis*.

Trichostrongylus vitrinus

Common name: Black scour worm

Description: Males measure around 4–6 mm and females 5–8 mm in length. The spicules are thick, unbranched, of equal length and end in a point (Fig. 1.13; Table 1.2c). Eggs are slightly 'brazil nut'-shaped and measure 93–118 by 41–52 µm.

Trichostrongylus capricola

Description: Males measure around 4–5 mm and females 6–7 mm in length. The male spicules are of equal length, thicker anteriorly than distally and end in a rounded tip (Table 1.2g).

Trichostrongylus falculatus

Description: Males measure around 4.5–5.5 mm. The spicules are thick, brown, of almost equal length with a sickle-shaped offshoot (Table 1.2f). The gubernaculum is bent anteriorly at right angles.

Fig. 1.13 Copulatory bursa and spicule of *Trichostrongylus vitrinus*. (Courtesy of Aránzazu Meana).

Trichostrongylus longispicularis

Description: Males are around 5.5 mm in length. The spicules are stout, brown, unbranched, and slightly unequal in length terminating in a tapering blunt tip that has a small semi-transparent membranous protrusion (Table 1.2d).

Trichostrongylus probolurus

Description: Males are 4.5–6.5 mm and females 6–7.5 mm in length. The spicules are large and of equal size with two triangular projections.

Trichostrongylus rugatus

Description: Males are 4.5–5.5 mm and females 4.5–7 mm in length. The spicules differ in size and dimensions and have a complex form with transverse ridges near the tip of the spicule (Table 1.2e).

Trichostrongylus retortaeformis

Description: The adults are small, white and hair-like, usually less than 7 mm long and difficult to see with the naked eye. In the male, the ventro-ventral ray tends to be disparate from the other rays and spicules are stout, unequal in length and terminate in a barb-like tip (Table 1.2h). The females possess double ovejectors. The medium-sized eggs are an irregular ellipse with dissimilar poles. One of the side walls may be slightly flattened (see Fig. 4.9). Eggs measure about 85–91 by 46–56 µm. The thin chitinous shell has a smooth surface and contains 16–32 blastomeres.

Trichostrongylus calcaratus

Description: The adults are small, white and hair-like, usually less than 7 mm long. Male worms have an asymmetrical dorsal ray and two short, nearly equal spicules.

Trichostrongylus affinus

Description: Males measure 5–7.5 mm and females 8.5–9 mm in length. The male spicules are short, broad and equal in length, bent ventrally and taper distally into two blunt hooks.

Trichostrongylus tenuis

Description: Males measure around 5–6.5 mm and females 7–9 mm in length. The spicules are curved distally and possess an auricular offshoot anteriorly. The worms have no buccal capsule. A useful generic character is the distinct excretory notch in the oesophageal region. The medium-sized eggs are long and ovoid with dissimilar poles and parallel side walls and are pale coloured with an almost colourless shell (see Fig. 4.8). They have a thin shell with a smooth surface and measure about 65–75 by 35–42 µm.

Life cycle: The prepatent period is short (7–10 days).

Marshallagia

Similar to *Ostertagia* spp. and can be differentiated by its greater length (males 10–13 mm; females 15–20 mm).

Life cycle: The life cycle is similar to *Ostertagia* except that L_2 can hatch from the egg. Following ingestion, larvae burrow into the abomasal mucosa and form small greyish white nodules, which may contain several developing parasites. The young L_5 emerge from the nodules around day 16 post infection and egg laying is usually apparent by three weeks. Arrested development of larvae can occur. The main species is *Marshallagia marshalli* which infects the abomasum of sheep, goats, deer and camels.

Marshallagia marshalli

Synonyms: *Ostertagia tricuspis*, *Ostertagia marshalli*

Description: Males have a long thin dorsal ray, which bifurcates near the posterior extremity (Fig. 1.14). The end of the spicule is divided into three small processes (Fig. 1.15), surrounded by a transparent membrane. The ellipsoidal eggs are much larger than those of *Ostertagia* spp., measuring 160–200 by 75–100 µm, and resemble those of *Nematodirus battus*. The thick-shelled eggs have almost parallel sides and contain a morula in an advanced stage of development when passed in the faeces (see Fig. 4.4). The eggs can be differentiated from those of *Nematodirus* as the morula is more developed and the geographical distribution of the worms is different.

Hyostrongylus

Slender reddish worms when fresh, with males measuring around 5–7 mm and females 6–10 mm in length (Fig. 1.16). The body cuticle is both transversely and longitudinally striated with 40–45 longitudinal striations.

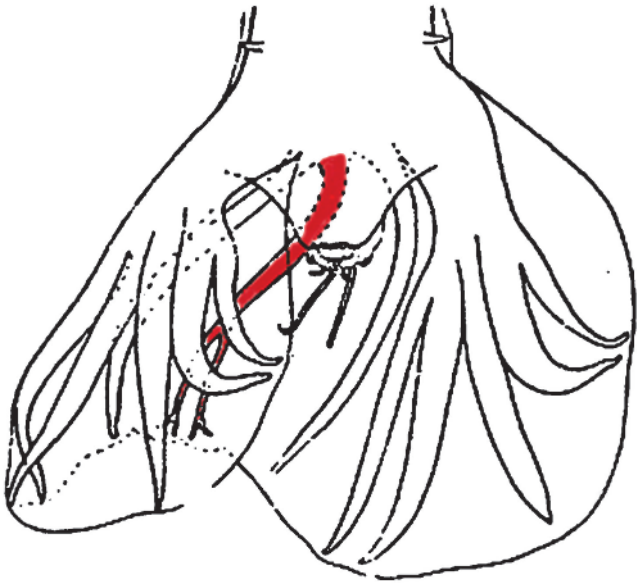


Fig. 1.14 Copulatory bursa of *Marshallagia marshalli* highlighting long thin bifurcating dorsal ray. (Adapted from Ransom, 1907.)

Fig. 1.15 Spicules of *Marshallagia marshalli*. (Adapted from Ransom, 1907.)

Life cycle: The free-living and parasitic stages are similar to those of *Ostertagia* in cattle; infection is through oral ingestion of L_3. The prepatent period is about three weeks. Hypobiosis of L_4 may occur following repeated infection, or be induced by seasonal changes, and is often seen in older animals. In sows, these hypobiotic larvae may resume their development during the periparturient relaxation of immunity and/or early lactation, leading to an increase in the faecal egg count. The main species is *Hyostrongylus rubidus* which infects the stomach of pigs.

Hyostrongylus rubidus

Description: Slender reddish worms when fresh, males measuring around 5–7 mm and females 6–10 mm in length (see Fig. 1.16). The body cuticle is both transversely and longitudinally striated with 40–45 longitudinal striations. A small cephalic vesicle is present and the spicules resemble *Ostertagia* in ruminants, but have only two distal branches. The bursa of the male is well developed and the dorsal lobe small. There is a well-developed telamen and short spicules. The vulva of the female opens in the posterior third of the body. Eggs are medium-sized, 71–78 by 35–42 µm, strongyle type and often difficult to differentiate from those of *Oesophagostomum*. They are ovoid with almost similar rounded poles and slightly barrel-shaped side walls. The eggshell is colourless with a thin wall and in fresh faeces contains a minimum of 32 blastomeres.

Mecistocirrus

Worms of this genus are similar in appearance to *Haemonchus contortus*, except that in the female the slit-shaped flapless vulva is located close to the anus. The males measure up to around 30 mm

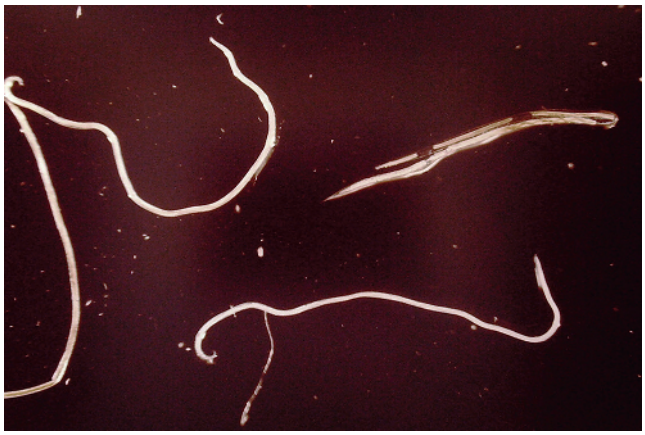


Fig. 1.16 Adult worms of *Hyostrongylus rubidus*.

and the females 42 mm in length. The cuticle contains many longitudinal ridges and the paired cervical papillae are readily apparent. The small buccal capsule is armed with a small lancet. In the female the ovaries are spirally coiled round the intestine, similar to *Haemonchus*. The male spicules are thin and long and in the bursa the dorsal ray is located symmetrically.

Life cycle: This is direct and similar to that of *Haemonchus*. The prepatent period is longer than in *Haemonchus*, being 60–80 days, partly the result of the longer duration of the fourth stage in the abomasal mucosa. The main species is *Mecistocirrus digitatus* which infects the abomasum of cattle, buffalos, sheep, goats and pigs.

Mecistocirrus digitatus

Description: To the naked eye, the worm is indistinguishable from *Haemonchus contortus*, although it is closely related to *Nematodirus*. The white ovary is wrapped around the red blood-filled intestine, giving it a 'barber's pole' appearance. The males measure up to around 30 mm and the females 42 mm in length. The male is distinguishable from *Haemonchus* by the presence of long narrow spicules that are fused together for the majority of their length and the tips are enclosed in a spindle-shaped appendage (in *Haemonchus* the spicules are thicker, separate and barbed at the tips). The dorsal ray is symmetrically located in the bursa, whereas in *Haemonchus* the dorsal ray is asymmetrical. The female differs from *Haemonchus* in that the slit-shaped vulva is positioned nearer to the tip of the tail and there is no vulval flap. The cuticle contains many longitudinal ridges and the cervical papillae are readily apparent. The small buccal capsule is armed with a lancet. The eggs are large and, unlike *Nematodirus*, typically strongylate and measure around 100 µm in length.

Graphidium

Stomach worms of lagomorphs found throughout Europe.

Life cycle: The life cycle is direct. Infection is by ingestion of infective larvae, which develop to the adult stage in the stomach in about 12 days. The main species is *Graphidium strigosum* which infects the stomach and small intestine of rabbits and hares.

Graphidium strigosum

Description: The adults are reddish worms when fresh, with 40–60 longitudinal lines and fine transverse striations. The male is 8–16 mm and female 11–20 mm long. The male bursa has large lateral lobes and a small dorsal lobe. Spicules are long, slender and each ends distally in several points. The medium-sized eggs are typically trichostrongyle, ovoid and measure 98–106 by 50–58 µm (see Fig. 4.9). The egg contains a large number of blastomeres or may contain an L_1 larva. The eggs are larger than those of *Trichostrongylus*.

Obeliscoides

This genus contains several species of worms found in a number of rabbit species in the USA.

Life cycle: The life cycle is direct. Infection is by ingestion of infective larvae, which develop to the adult stage in the stomach in about 19 days. The main species is *Obeliscoides cuniculi* which infects the stomach of rabbits, hares and occasionaly white-tailed deer.

Obeliscoides cuniculi

Description: Adults are red-brownish in colour and males measure 10–16 mm and the females 15–18 mm in length. The brown spicules are bifurcated at their distal tips and terminate in a hook. The female worm tapers in the distal 20% of the body. The male spicules are brown and bifurcated at the distal end. The body of the female is tapered over the posterior 20% of its length. Eggs are typically trichostrongyle, ovoid and measure 76–86 by 44–45 µm (see Fig. 4.9).

Libyostrongylus

Libyostrongylus douglassi and *Libyostrongylus dentatus* are parasites of ratites (ostrich) commonly referred to as 'Wireworms' found in the proventriculus and gizzard.

Life cycle: The life cycle is typically strongyle. Following ingestion, infective larvae burrow into the proventricular glands and under the kaolin layer of both the proventriculus and gizzard where they develop into adult worms 4–5 weeks later. Eggs which contain fully developed larvae are very resistant to desiccation and can survive a couple of years.

Libyostrongylus douglassi

Description: Small yellowish-red nematodes, males 4–6 mm and females 5–6 mm in length. The male bursa is well developed; the dorsal ray is long and split in its distal half forming three small branches either side. The spicules each end in a large and small spine. Eggs measure 59–74 by 36–44 µm. Third-stage larvae are characterised by a small knob at the tip of the tail and measure around 745 µm in length (Fig. 1.17).

Libyostrongylus dentatus

Description: Males are 6–8 mm and females 10–12 mm in length. There is a prominent dorsal, oesophageal tooth. The male has a large bursa; the dorsal ray is long and bifurcated, extending into a

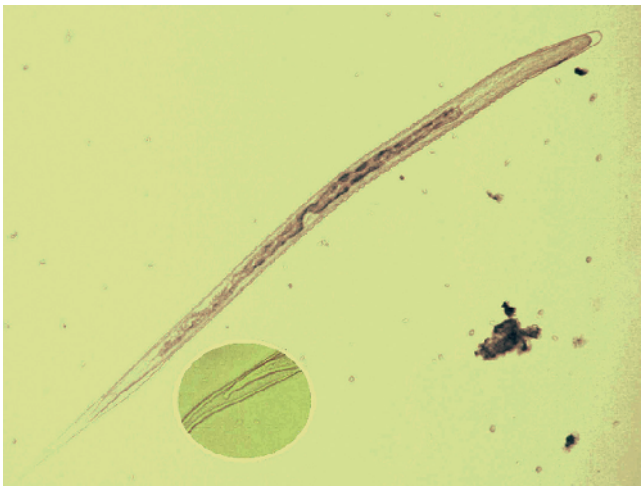


Fig. 1.17 *Libyostrongylus douglassi* L_3. Inset shows magnified larval tail tip within the third cuticle.

rounded lobe of the bursal membrane. The spicules have a dorsal process arising two-thirds from the anterior and the main shaft ending in a rounded point capped by a hyaline sheath.

Graphinema

Graphinema aucheniae

Description: Male worms measure 5.5–8 mm and females 9–12 mm in length. These worms have a small buccal capsule, a claviform oesophagus and cervical papillae. The male bursa has a small anteroventral ray and a widely divergent posteroventral ray. The dorsal ray bifurcates near the distal tip, with each branch dividing distally. The spicules are long and pointed.

Life cycle: Similar to that of other trichostrongyles. The main species is *Graphinema aucheniae* which infects the abomasum of llamas and vicunas.

Impalaia

Impalaia tuberculata and *Impalaia nudicollis* are parasites of the abomasum of camels, very similar in dimensions (i.e. males are 7–9 mm and females 14–18 mm long). *Impalaia tuberculata* has the cervical cuticle studded with papillae and spicules are equal in length, slender and with a fine pointed end, whereas *Impalaia nudicollis* males have long spicules and a long gubernaculum.

SUBFAMILY OSTERTAGINAE

Species within the subfamily Ostertaginae are considered together as they form a large and complex group, the taxonomy of which has not been fully elucidated. Some species names are considered synonymous and species polymorphism is commonly reported (Table 1.4).

The adults are slender reddish-brown worms up to 1 cm long, occurring on the surface of the abomasal mucosa and are only visible on close inspection (Fig. 1.18). They possess a short buccal cavity and a very small pair of cervical papillae. The short spicules

Table 1.4 *Ostertagia* species.

Species	Hosts	Site
Ostertagia ostertagi *Ostertagia* (syn. *Skrjabinagia*) *lyrata*	Cattle, deer, rarely goats	Abomasum
Ostertagia leptospicularis (syn. *Ostertagia crimensis*) *Skrjabinagia* (*Ostertagia*) *kolchida* (syn. *Grosspiculagia podjapolskyi*)	Deer, cattle, sheep and goats	Abomasum
Teladorsagia circumcincta *Ostertagia trifurcata* *Teladorsagia davtiani*	Sheep, goats, deer, camels, llamas	Abomasum
Spiculopteragia spiculoptera (syn. *Apteragia spiculoptera*, *Rinadia spiculoptera*, *Mazamostrongylus spiculoptera*)	Deer (red deer, fallow deer, roe deer), cattle, sheep, goats	Abomasum
Spiculopteragia asymmetrica (syn. *Ostertagia asymmetrica*, *Apteragia asymmetrica*, *Rinadia asymmetrica*, *Mazamostrongylus asymmetrica*)	Deer (roe deer, sika deer, fallow deer)	Abomasum
Apteragia quadrispiculata	Deer (roe deer, sika deer, fallow deer)	Abomasum
Spiculopteragia (*Apteragia*) *bohmi* *Spiculopteragia* (*Rinadia*) *mathevossiani*	Mouflons, deer (fallow deer, roe deer)	Abomasum
Spiculopteragia peruvianus	Llamas, vicunas	Abomasum

are brown in colour and terminate in two or three processes, depending on the species. In the female, the vulva can be covered with a flap or this may be absent and the tip of the tail is annulated.

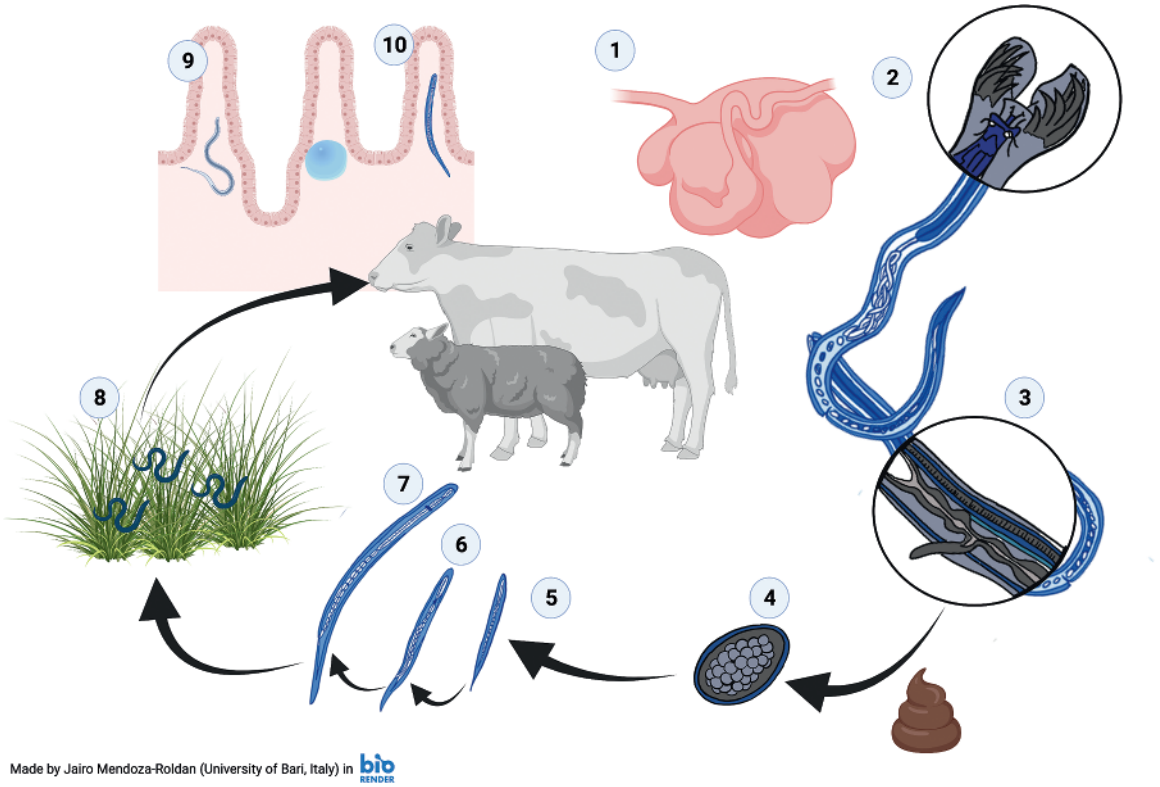
The larval stages occur in the gastric glands and can only be seen microscopically following processing of the gastric mucosa. Species differentiation is generally based on the structure of the male spicules. These worms occur in cattle, sheep and other ruminants.

Life cycle: Eggs are passed in the faeces and, under optimal conditions, develop within the faecal pat to the infective third stage within two weeks. When moist conditions prevail, the L_3 migrate from the faeces on to the herbage. After ingestion, the L_3 exsheaths in the rumen and further development takes place in the lumen of an abomasal gland. Two parasitic moults occur before the L_5 emerges from the gland around 18 days after infection to become sexually mature on the mucosal surface. The entire parasitic life cycle usually takes tyree weeks, but under certain circumstances many of the ingested L_3 become arrested in development at the early fourth larval stage (EL_4) for periods of up to six months (also referred to as hypobiosis). See **life cycle 1**.

Fig. 1.18 *Ostertagia ostertagi* on the abomasal mucosa.

LIFE CYCLE 1. LIFE CYCLE OF *OSTERTAGIA* SPP.

Adults of *Ostertagia* spp. live on the surface of the abomasum (1) of cattle and small ruminants. Worms are thin and whitish in colour, with a vestigial buccal capsule. Males are ~7 mm long and characterised by a well-developed copulatory bursa and distinct spicules, whose morphology is useful for species identification (2). Females are ~11 mm long, and in some species the vulva is covered by a cuticular expansion known as a 'vulvar flap' (3). The eggs are elliptical in shape, thin-walled and transparent (80–100 × 50 µm), with 16–32 blastomeres (4); eggs are eliminated into the environment with the faeces. Under optimal conditions of temperature and humidity, eggs hatch into L_1 (5) which, after two moults, develop into second-stage (6) and infective third-stage larvae (L_3) (7). Once ingested by grazing ruminants (8), the larvae lose their external sheath in the rumen and travel to the abomasum, where they penetrate the gastric glands (9) and continue their development. Here, the L_3 moult to L_4 and grow from 1.3 mm to 8 mm in length, thus forming nodules ~1–2 mm in diameter with a characteristic central hole; the glandular mucosa appears hyperplasic and undergoes functional changes that lead to a significant reduction in the production of gastric pepsin. During winter, the larvae can undergo hypobiosis (reduced metabolism and developmental arrest). The larvae develop to L_5 (10) and emerge in the lumen of the abomasum. The prepatent period, from ingestion of infective larvae to development of sexually mature adults, takes ~3 weeks. The life cycle of other Trichostrongylidae is similar to that of *Ostertagia* spp., except for *Nematodirus* spp. whose infective L_3 develop inside the eggs, prior to hatching in the environment.



Ostertagia ostertagi

Morph species: *Ostertagia* (syn. *Skrjabinagia*) *lyrata*

Description: Adults are small, slender reddish-brown worms with a short buccal cavity. Males measure 6–8 mm and females 8–11 mm in length. The cuticle in the anterior region is striated transversely whereas the rest of the body is unstriated and bears around 30 longitudinal ridges.

- *Ostertagia ostertagi*: The spicules are divided in the posterior region where two thin lateral branches arise from the main stem (Table 1.5a). The bursa is small and the accessory bursal membrane is supported by two divergent rays (Fig. 1.19). In the female, the vulva is sited about 1.5 mm from the posterior and is covered with a flap (Fig. 1.20).
- *Ostertagia lyrata*: The spicules are stout and divided into three branches posteriorly. The main branch is solid and ends in a shoe-like expansion. One lateral branch is thick and massive, terminating in a hat-like expansion; the other is small and pointed (Table 1.5b and Fig. 1.21). The gubernaculum is spindle-shaped.

Ostertagia leptospicularis

Synonym: *Ostertagia crimensis*

Morph species: *Skrjabinagia* (*Ostertagia*) *kolchida* (syn. *Grossiculagia podjapolskyi*)

Description: Adults are slender reddish-brown worms with a short buccal cavity. Males measure 6–8 mm and females 8–9 mm in length.

Table 1.5 Identification of Ostertaginae based on male spicule morphology.

Species	Spicules: description	Spicules: morphology
Ostertagia ostertagi	The spicules are of equal length and shape, tapering towards the distal end into three processes	(a) 
Ostertagia lyrata	The spicules are stout and divided into three branches posteriorly. The main branch is solid and ends in a shoe-like expansion. One lateral branch is thick and massive, terminating in a hat-like expansion; the other is small and pointed	(b) 
Ostertagia leptospicularis	The spicules are slender, of equal length and shape, tapering towards the distal end into three processes, with the two lateral branches extremely fine and pointed	(c) 
Skrjabinagia kolchida	The spicules are of equal length and shape, tapering towards the distal end into three branches terminating in an 'ice-skate'-like structure. The medial branch is the shortest and truncated	(d) 
Teladorsagia circumcincta	Spicules are variable in length but normally long and thin. The posterior end is split into two branches of equal length. A third short offshoot, not readily seen, arises in front of the bifurcation	(e) 
Ostertagia trifurcata	Spicules are short and broad; the posterior end is divided into three processes, one long and thick with a truncated end, and two short slender branches each tapering to a point	(f) 
Spiculopteragia spiculoptera	The spicules are of equal length, bifurcating distally where they contain a cavity and distally ending in a fan-shaped expansion	(g) 
Spiculopteragia bohmi	Spicules of equal size but asymmetrical. The right spicule divides into three branches and the left spicule into two branches	(h) 

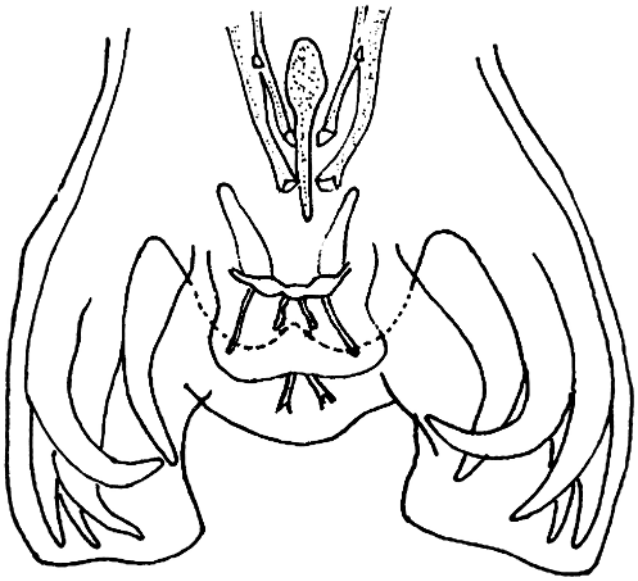


Fig. 1.19 Male bursa and spicules of *Ostertagia ostertagi*.

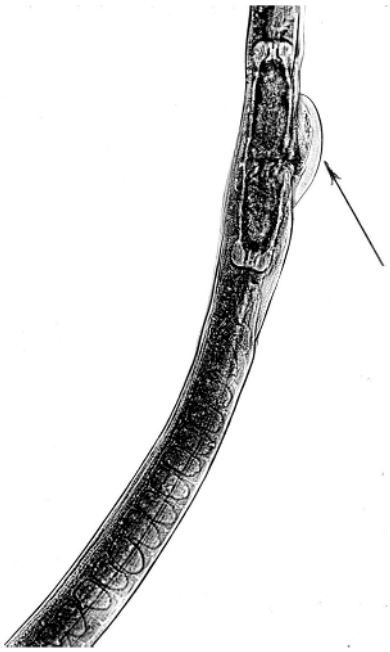


Fig. 1.20 Female vulva and flap (arrowed) of *Ostertagia ostertagi*.

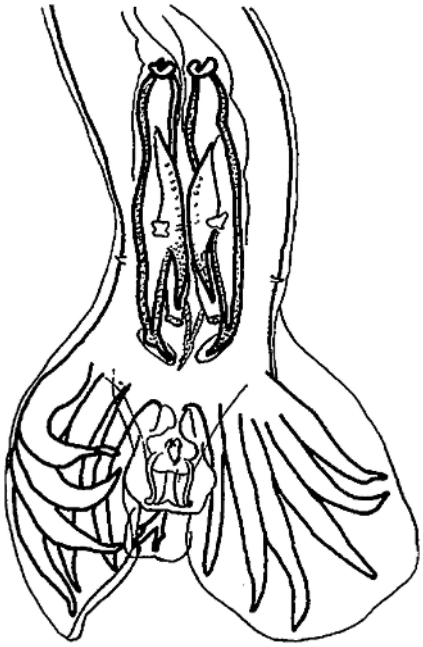


Fig. 1.21 Male bursa and spicules of *Ostertagia lyrata*.

Distinguished from other ostertagian species by the length of the oesophagus, which is longer (0.7 mm compared with approximately 0.6 mm in other species). In cattle, the worms are thinner than *O. ostertagi* and male worms are differentiated on spicule morphology.

- *Ostertagia leptospicularis*: The spicules are of equal length and shape, tapering towards the distal end into three processes (Table 1.5c and Fig. 1.22). The gubernaculum is racket-shaped.
- *Skrjabinagia kolchida*: The spicules are of equal length and shape, tapering towards the distal end into three branches terminating in a shoe-like structure (Table 1.5d and Fig. 1.23). The medial branch is the shortest and truncated. The gubernaculum is longer than in *O. leptospicularis* and twisted.

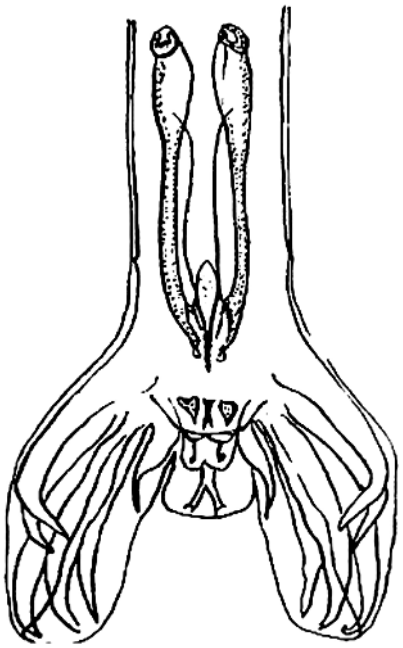


Fig. 1.22 Male bursa and spicules of *Ostertagia leptospicularis*.

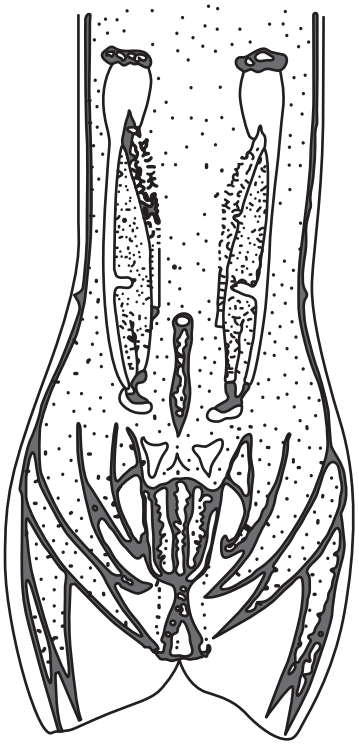


Fig. 1.23 Male bursa and spicules of *Skrjabinagia kolchida*.

Teladorsagia circumcincta

Synonym: *Ostertagia circumcincta*

Morph species: *Ostertagia trifurcata*, *Teladorsagia davtiani*

Description: Adults are slender reddish-brown worms with a short buccal cavity. Males measure 6–8 mm and females 8–10 mm.

- *Teladorsagia circumcincta*: The lateral lobes of the bursa are well developed but the dorsal lobe is small; a telamon is present in the genital cone; the accessory bursal membrane is small and supported by two divergent rays (Fig. 1.24). Spicules are variable in length but

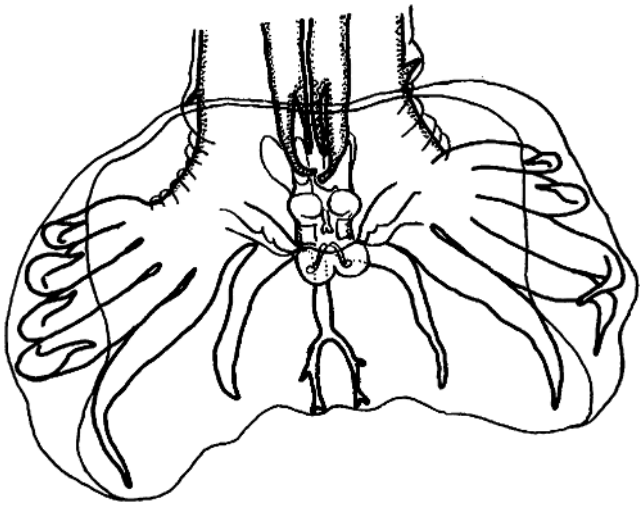


Fig. 1.24 Male bursa and spicules of *Teladorsagia circumcincta*.

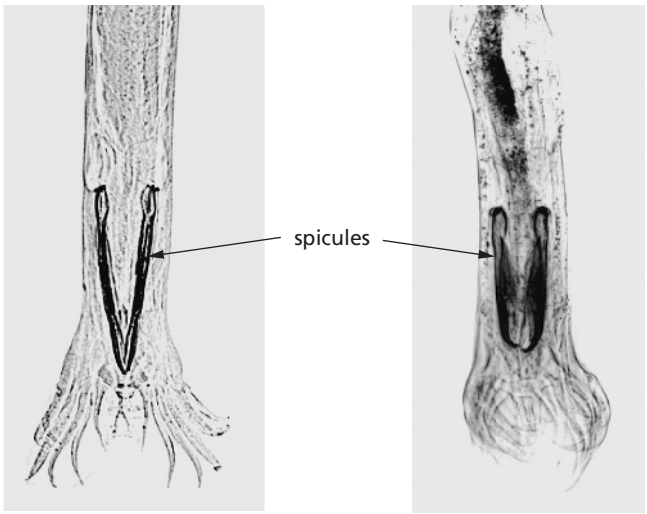


Fig. 1.25 Comparison of spicules of (a) *Teladorsagia circumcincta* and (b) *Ostertagia trifurcata*. Those of *T. circumcincta* are long and thin whereas *O. trifurcata* spicules are short and broad.

normally long and thin (Table 1.5e and Fig. 1.25a). The posterior end is split into two branches of equal length. A third short offshoot, not readily seen, arises in front of the bifurcation. The gubernaculum is racket-shaped. In the female, the vulva is usually covered with a large flap and opens near the posterior of the body.

- *Ostertagia trifurcata*: The bursa is longer than in *T. circumcincta*. The lateral lobes of the bursa are well developed and the dorsal lobe is small (Fig. 1.26). A well-developed telamon is present in the genital cone. The accessory bursal membrane is modified to form Sjoberg's organ supported by two rays. The spicules are short and broad (Table 1.5f and Figs 1.25b and 1.26) with the posterior ends divided into three processes, one long and thick with a truncated end and two short slender branches each tapering to a point. The gubernaculum is somewhat spindle-shaped.
- *Teladorsagia davtiani*: This morph species is similar in appearance to *O. trifurcata*. The accessory bursal membrane is modified to form Sjoberg's organ and resembles a pair of sessile papillae on the posterior extremity of the genital cone (Fig. 1.27).

Spiculopteragia spiculoptera

Synonyms: *Apteragia spiculoptera*, *Rinadia spiculoptera*, *Mazamostrongylus spiculoptera*

Description: The spicules are of equal length, bifurcating distally where they contain a cavity, and distally ending in a fan-shaped expansion (Table 1.5g). The gubernaculum is absent.

Spiculopteragia asymmetrica

Synonyms: *Ostertagia asymmetrica*, *Apteragia asymmetrica*, *Rinadia asymmetrica*, *Mazamostrongylus asymmetrica*

Description: Males measure 4.5–6 mm. Spicules are distally asymmetrical and pointed, with a T-shaped offshoot near the distal end of the right spicule. The gubernaculum is small and boat-shaped.

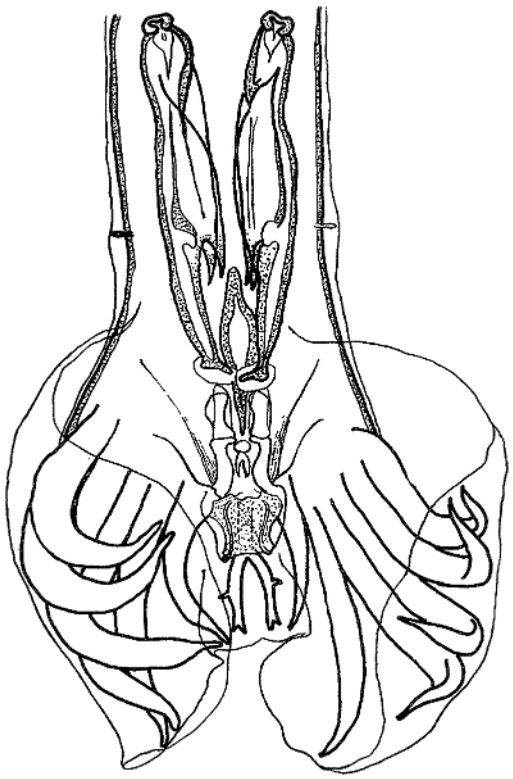


Fig. 1.26 Male bursa and spicules of *Ostertagia trifurcata*.

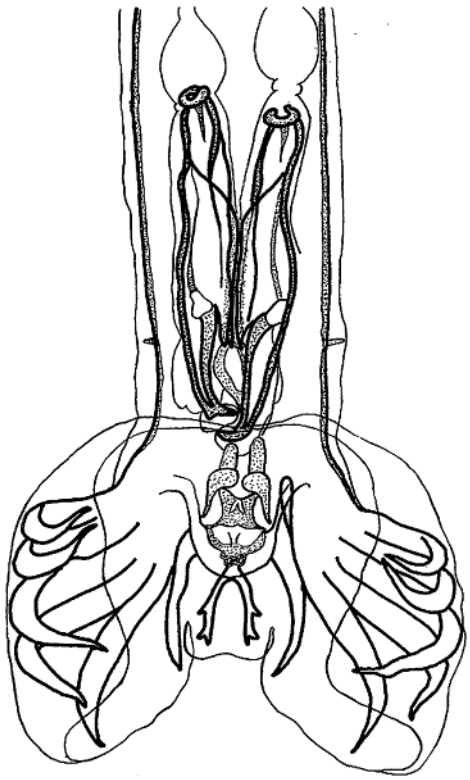


Fig. 1.27 Male bursa and spicules of *Teladorsagia davtiani*.

Apteragia quadrispiculata

Description: Males measure 6–8.5 mm. Spicules possess four branches distally.

Spiculopteragia bohmi

Synonyms: *Apteragia bohmi*, *Rinadia bohmi*, *Mazamostrongylus bohmi*, *Ostertagia bohmi*

Morph species: *Spiculopteragia* (*Rinadia*) *mathevossiani*

Description: Considered to be a polymorphic species with two male morphs, *Spiculoptergia bohmi* and *Spiculoptergia mathevossiani*. Males measure 6–7 mm.

- *Spiculopteragia bohmi*: Spicules of equal size but asymmetrical. The right spicule divides into three branches and the left spicule into two branches (Table 1.5h). The gubernaculum is absent.
- *Spiculopteragia mathevossiani*: The spicules have asymmetrical distal thirds each ending in three branches. The gubernaculum is absent.

Spiculopteragia peruvianus

Description: Males measure 6.5–8 mm and females 8.5–10 mm in length.

Camelostrongylus

The main species is *Camelostrongylus mentulatus* which infects the abomasum and small intestine of camels, sheep and goats.

Camelostrongylus mentulatus

Synonym: *Ostertagia mentulatus*

Description: *Camelostrongylus mentulatus* is similar in size to *Ostertagia ostertagi*. Males are 6.5–7.5 mm and females 8–10 mm long. The bursa possesses two large lateral lobes and the spicules are narrow, long, denticulated and of equal length (Fig. 1.28). Eggs measure about 75–85 by 40–50 µm.

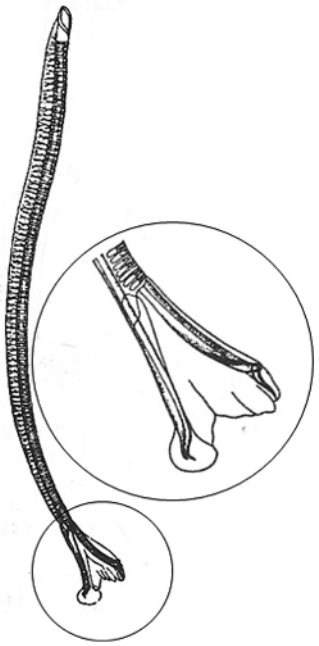


Fig. 1.28 Male bursa and spicule of *Camelostrongylus mentulatus*. (Adapted from Skrjabin *et al*., 1954.)

SUBFAMILY HAEMONCHINAE

Haemonchus

The adult *Haemonchus* spp. (Table 1.6) are easily identified because of their specific location in the abomasum and their large size (2–3 cm). In fresh female specimens, the white ovaries winding spirally around the blood-filled intestine produce a 'barber's pole' appearance (Fig. 1.29). The buccal cavity is small and contains a small lancet-like tooth. The anterior body possesses prominent cervical papillae. The vulva is usually protected by a cuticular flap which can have a range of shapes. In the male, the lateral lobes of the bursa are large, whereas the dorsal ray is small and asymmetrical.

Table 1.6 *Haemonchus* species.

Species	Hosts	Site
Haemonchus contortus (syn. *Haemonchus placei*)	Sheep, goats, cattle, deer, camels, llamas	Abomasum
Haemonchus similis	Cattle, deer	Abomasum
Haemonchus longistipes	Camels, sheep	Abomasum

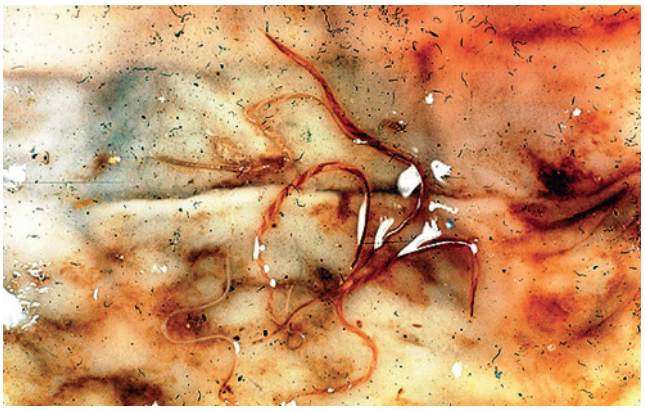


Fig. 1.29 Adult male and female worms of *Haemonchus contortus* on the abomasal mucosa.

Life cycle: This is direct and the preparasitic phase is typically trichostrongyloid. The females are prolific egg layers. The eggs hatch to L_1 on the pasture and may develop to L_3 in as little as five days but development may be delayed for weeks or months under cool conditions. After ingestion and exsheathment in the rumen, the larvae moult twice in close apposition to the gastric glands. Just before the final moult, they develop the piercing lancet which enables them to obtain blood from the mucosal vessels. As adults, they move freely on the surface of the mucosa. The prepatent period is 2–3 weeks in sheep and four weeks in cattle.

Haemonchus contortus

Synonym: *Haemonchus placei*

Description: Males are about 10–22 mm and females 20–30 mm in length. The male has an asymmetrical dorsal lobe and barbed spicules (Fig. 1.30a). The vulva is situated at the beginning of the posterior third of the body. This is a useful feature for distinguishing *Haemonchus* from *Mecistocirrus*, in which the vulva is positioned near the tip of the tail. In both sexes there are cervical papillae (Fig. 1.30b) and a tiny lancet inside the buccal capsule. Infective larvae have 16 gut cells, the head is narrow and rounded and the tail of the sheath is offset. The egg is medium-sized (64–95 × 40–50 µm) and is a regular broad ellipse with barrel-shaped side walls and flattened wide poles (see Fig. 4.4). The chitinous shell is thin, slightly light-yellowish in colour and smooth, and the egg contains numerous blastomeres which nearly fill the entire volume. The blastomeres are not readily distinguished. Infective larvae measure around 690 µm (see Fig. 4.15).

Notes: Until recently, the sheep species was *H. contortus* and the cattle species *H. placei*. However, there is now increasing evidence that these are the single species *H. contortus* with only strain adaptations for cattle and sheep.

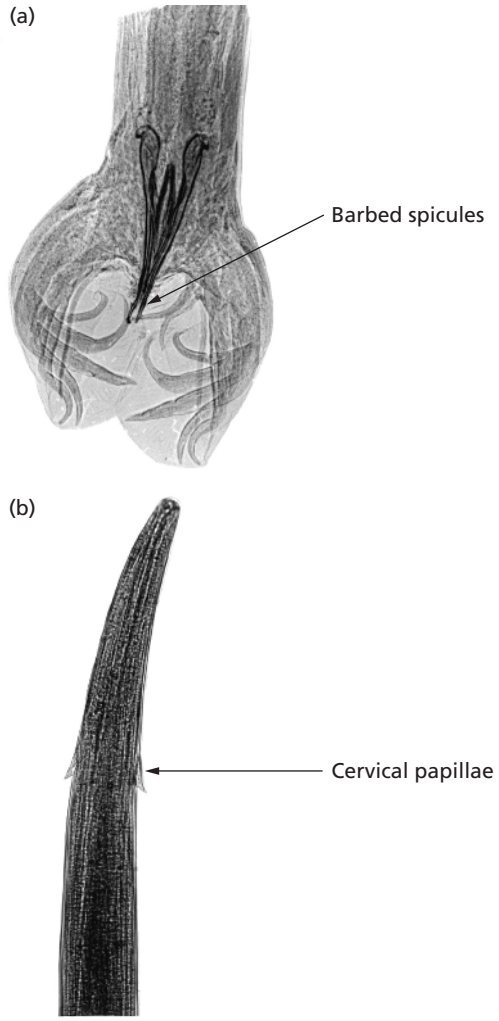


Fig. 1.30 (a) Barbed spicules and bursa of a mature *Haemonchus contortus* male worm. (b) Anterior of *H. contortus* showing the position of the cervical papillae.

Haemonchus similis

Description: The adults are 2–3 cm and reddish in colour. The male has an asymmetrical dorsal lobe and barbed spicules, differing from *H. contortus* in that the terminal processes of the dorsal ray are longer and the spicules shorter.

Haemonchus longistipes

Description: Relatively small worms; males are 10–20 mm and females 18–30 mm long. Females have a reduced knob-like vulval flap (cf. *H. contortus* which has a well-developed linguiform vulvar flap).

FAMILY COOPERIDAE

Cooperia

Cooperia spp. (Table 1.7) are relatively small worms (usually less than 9 mm long), which appear pinkish-white when fresh. The main generic features are the small cephalic vesicle and the marked transverse cuticular striations in the oesophageal region (Fig. 1.31). The body possesses longitudinal ridges. The male bursa is relatively

Table 1.7 *Cooperia* species.

Species	Hosts	Site
Cooperia oncophora	Cattle, sheep, goats, deer, camels	Small intestine
Cooperia curticei	Sheep, goats, deer (red deer, fallow deer)	Small intestine
Cooperia punctata	Cattle, deer, rarely sheep	Small intestine
Cooperia pectinata	Cattle, deer, rarely sheep	Small intestine
Cooperia surnabada (syn. *Cooperia mcmasteri*)	Cattle, sheep, goats, camels	Small intestine

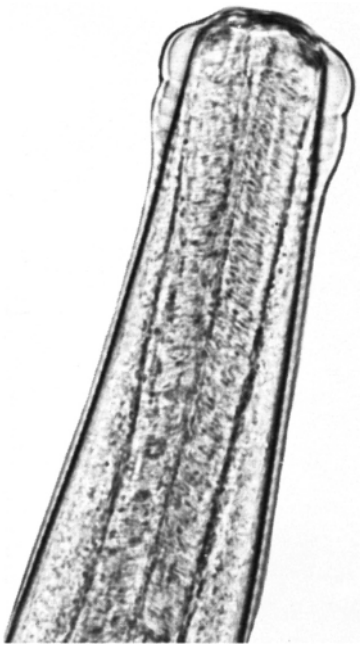


Fig. 1.31 Anterior of *Cooperia* spp. showing the cephalic vesicle and cuticular striations.

large compared to the size of the body. It has a small dorsal lobe, and the brown-coloured spicules are short and stout with distinct wing-like expansions in the middle region, which often bear transverse ridged striations (except in *C. surnabada*) (Table 1.8). There is no gubernaculum. The females have a long tapering tail and the vulva may be covered by a vulval flap and is located posterior to the middle of the body. The egg contains many blastomeres that are not easily distinguished. The small poles are very similar and the side walls are parallel. This feature allows the eggs to be differentiated from those of *Ostertagia* which have wider poles and more spherical walls.

Life cycle: The life cycle is direct and typical of the superfamily. Ingested L_3 exsheath, migrate into the intestinal crypts for two moults and then the adults develop on the surface of the intestinal mucosa. The prepatent period is 2–3 weeks. The bionomic requirements of the free-living stages are similar to those of *Teladorsagia*.

Cooperia oncophora

Description: In size, *C. oncophora* is similar to *Ostertagia* but with a large bursa. Males measure around 5.5–9 mm and females 6–8 mm in length. Spicules have a longitudinal line pattern with the distal end rounded and bearing cuticular formations (Table 1.8a).

Cooperia curticei

Description: *Cooperia curticei* is moderately small with a large bursa with fleshy supporting rays. The most notable feature is the 'watch spring'-like posture. Males measure around 4.5–6 mm and females 6–8 mm in length. When fresh, they appear pinkish white. The main generic features are the very small cephalic vesicle and the transverse cuticular striations in the oesophageal region. The body possesses longitudinal ridges. Spicules are equal in length and have a central protuberance with a transverse striation and end in a rounded disc-like structure (Table 1.8b). The females have a long tapering tail. Eggs are oval with nearly similar poles and parallel side walls (see Fig. 4.4). They are thin-shelled with a smooth surface and contain many blastomeres which are hard to distinguish. Infective larvae measure around 780 µm (see Fig. 4.15).

Cooperia surnabada

Synonym: *Cooperia mcmasteri*

Description: The males measure around 7 mm and the females 8 mm in length. The appearance is very similar to *C. oncophora*, although the bursa is larger and the bursal rays tend to be thinner. The spicules are thinner with a posterior bifurcation into an external branch with a small conical appendage and an internal branch that is shorter and pointed (Table 1.8c).

Cooperia punctata

Description: Males measure around 4.5–6 mm and females 6–8 mm in length. Spicules are short and bear a large protuberance at the distal half, tapering to a slightly blunted point (Table 1.8d).

Table 1.8 Identification of *Cooperia* spp. based on male spicule morphology.

Species	Spicules: description	Spicules: morphology
Cooperia oncophora	Spicules are 240–300 µm long and have a longitudinal line pattern with the distal end rounded and bearing cuticular formations	(a) 
Cooperia curticei	Spicules are equal in length (135–145 µm) and have a central protuberance with a transverse striation and end in a rounded 'disc-like' structure	(b) 
Cooperia surnabada	The spicules are 270 µm long and thin with a posterior bifurcation into an external branch with small conical appendage and an internal branch that is shorter and pointed	(c) 
Cooperia punctata	Spicules are short (120–150 µm) and bear a large protuberance at the distal half, tapering to a slightly blunted point	(d) 
Cooperia pectinata	Spicules are 240–280 µm long with a large protuberance centrally, and are bent ventrally, with a wrinkled inner surface	(e) 

Cooperia pectinata

Description: Males measure around 7–8 mm and females 7.5–10 mm in length. Spicules bear a protuberance centrally and are bent ventrally, with a wrinkled inner surface (Table 1.8e).

FAMILY ORNITHOSTRONGYLIDAE

Ornithostrongylus

The adult worms, which measure up to 2.5 cm, are bloodsuckers, have a reddish colour and can be seen by the naked eye. The life cycle is direct and typically trichostrongyle. The main species is *Ornithostrongylus quadriradiatus* which infects the crop, proventriculus and small intestine of pigeons and doves.

Ornithostrongylus quadriradiatus

Description: Males measure 9–12 mm and females 18–24 mm in length. The cuticle of the head is slightly inflated and the body bears longitudinal cuticular ridges. The anterior of the worm has a long, slightly inflated vesicle, which is present from the cephalic area to the cervical region. The tail of the female worm is blunt with a small spine. In the male bursa, the ventral rays are close together and the dorsal ray is short. The telamon is shaped like a small bar with two arms and covers the tips of the spicules. Spicules end in three pointed processes. Eggs are ovoid and measure 70–75 by 38–40 µm.

FAMILY AMIDOSTOMIDAE

Amidostomum

The slender adult worms, bright red in colour when fresh and up to 2.5 cm in length, are easily recognised at necropsy where they predominate in the horny lining of the gizzard (Fig. 1.32). These worms have a shallow buccal cavity and do not possess leaf crowns. Three longitudinal ridges/plates line the oesophagus.

Life cycle: Direct and similar to other strongyles. Infection is via ingestion of L_3 or through skin penetration. Eggs passed in the faeces are already embryonated and develop to L_3 in the egg. Ingested larvae penetrate the submucosa of the gizzard. Patency is around 2–3 weeks in geese.

Amidostomum anseris

Synonym: *Amidostomum nodulosum*

Description: The slender adult worms, bright red in colour when fresh and up to 2.5 cm in length, are easily recognised at necropsy where they predominate in the horny lining of the gizzard. Males measure about 10–17 mm and females 15–25 mm. Characterised by a shallow buccal capsule with three pointed teeth, the middle one being the largest. The male spicules are of equal length and are divided into two branches at the posterior. The medium-sized eggs are thin-shelled with a smooth surface, ellipsoidal and measure around 90–110 by 50–80 µm and contain a large number of blastomeres or a segmented embryo when laid (see Fig. 4.8). The egg hatches when the L_3 larva is present.

Amidostomum acutum

Synonym: *Amidostomum skrjabini*

Description: Characterised by a shallow buccal capsule with one pointed tooth. The spicules have 2–3 branches at the distal end.

Epomidiostomum

These worms are similar to *Amidostomum* but smaller.

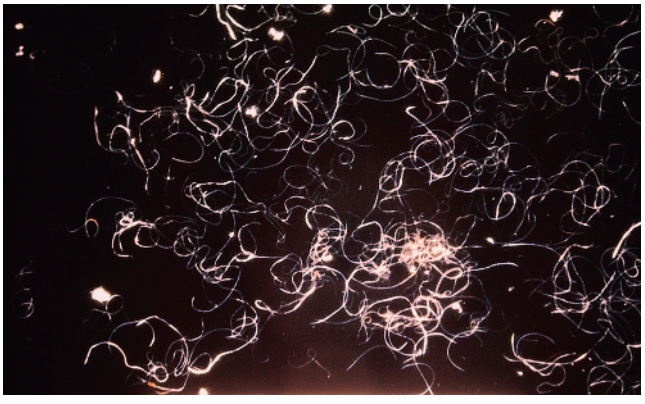


Fig. 1.32 Adult worms of *Amidostomum anseris*.

Epomidiostomum uncinatum

Synonyms: *Epomidiostomum anatinum*, *Strongylus uncinatus*, *Amidostomum anatinum*

Description: Males measure about 10 mm and females 15 mm in length. Teeth are absent from the rudimentary buccal capsule. The cuticle bears distinct thickenings, 'epaulettes', at the anterior end and tooth-like projections form a fringe around the mouth. The posterior of the female is rounded and has a small button-shaped tip. Three branches occur on each spicule.

Epomidiostomum orispinum

Synonyms: *Strongylus anseris*, *Strongylus orispinum*
Description: Males measure around 11 mm and females 16 mm in length. The anterior of the worm possesses four posteriorly pointing offshoots and lateral festoons bearing a pair of papillae. Spicules are equal with three shafts pointing distally. The body of the female tapers abruptly, towards the digitate tail.

Epomidiostomum skrjabini

Description: The size of the males and females is similar to that of *E. orispinum*. The head of the worm possesses a cuticular prominence which is armed with four symmetrical, lateral-pointing spines. There are also two epaulette formations. The mouth is surrounded by four small spines. The bursa has three lobes, the central lobe being poorly developed. Spicules are equal and the posterior ends are split into three sharp-tipped branches. The anterior ends are blunt. The female tail terminates in a finger-like appendage, which is bent ventrally.

FAMILY MOLINEIDAE

Nematodirus

Nematodirus spp. adult worms (Table 1.9) are whitish, slender and relatively long, with the anterior thinner than the posterior region. They may appear slightly coiled. Adult males are 10–15 mm and females 15–24 mm in length. A small but distinct cephalic vesicle is present (Fig. 1.33) and the cuticle possesses about 14–18 longitudinal ridges. The male bursa has elongated lateral lobes and the spicules are long and slender; the tips of the spicules are fused together and terminate in a small expansion, which varies in shape and is a useful feature for species differentiation (Table 1.10). The ventral

Table 1.9 *Nematodirus* species.

Species	Hosts	Site
Nematodirus battus	Sheep, goats, occasionally cattle	Small intestine
Nematodirus filicollis	Sheep, goats, occasionally deer	Small intestine
Nematodirus spathiger	Sheep, goats, cattle	Small intestine
Nematodirus helvetianus	Cattle, occasionally sheep, goats	Small intestine
Nematodirus abnormalis	Camels, sheep, goats	Small intestine
Nematodirus mauritanicus	Camels	Small intestine
Nematodirus lamae	Llamas, alpacas, vicunas	Small intestine
Nematodirus leporis	Rabbits	Small intestine

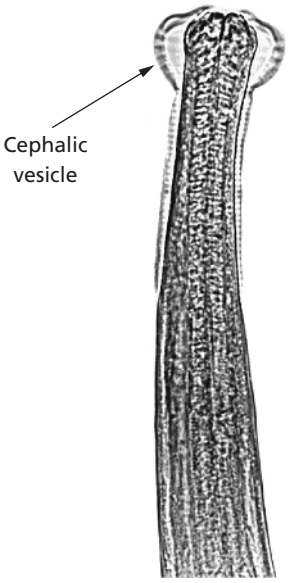


Fig. 1.33 Anterior of *Nematodirus battus* illustrating the small cephalic vesicle.

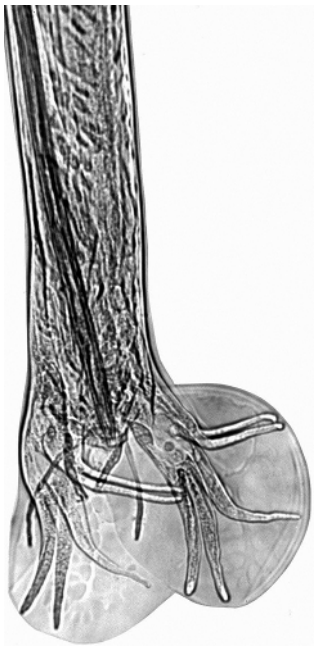


Fig. 1.34 Male bursa and spicules of *Nematodirus battus* with single sets of parallel rays in the dorsal lobes.

Table 1.10 Identification of *Nematodirus* species based on male spicule morphology.

Species	Spicules: description	Spicules: morphology
Nematodirus battus	The spicules are long and slender and the tips are fused into a small, flattened oval-shaped projection	(a)
Nematodirus filicollis	The spicules are long and slender with fused tips and terminate in a narrow pointed swelling	(b)
Nematodirus spathiger	The spicules are long and slender with fused tips and terminate in a spoon-shaped tip	(c)
Nematodirus helvetianus	The long slender spicules terminate in a fused point with the surrounding membrane being lanceolate	(d)
Nematodirus abnormalis	The spicules are asymmetrical with the distal ends bent to form an asymmetrical lancet	(e)

rays are parallel and are situated close together. The female worm has a short tail with a slender terminal appendage. The eggs are large and readily distinguishable from other trichostrongiloid species.

Life cycle: The preparasitic phase is almost unique in the trichostrongyloids in that development to the L_3 stage takes place within the eggshell. Species differences occur regarding the critical hatching requirements.

Nematodirus battus

Description: The adults are long and slender, the males measuring around 11–16 mm and females 15–25 mm in length. The anterior of the worm is thinner than the posterior region and the cuticle possesses longitudinal ridges. The body is usually twisted or coiled so that the worms tend to tangle together. A small but distinct cephalic vesicle is present (see Fig 1.33). Males are characterised by having only one set of divergent rays in each bursal lobe (Fig. 1.34) and the tips of the spicules are fused into a small, flattened, oval-shaped projection (Table 1.10a). The female worm has a long pointed tail. The large egg is brownish with parallel sides and measures around 150–180 by 67–80 µm (see Fig. 4.4). The chitinous eggshell is thin-walled, smooth and contains 4–8 darkly stained blastomeres when passed in faeces.

Life cycle: Development to the L_3 takes place within the eggshell. Hatching of most eggs requires a prolonged period of chill followed by a mean day/night temperature of more than 10 °C, conditions which occur in late spring in the northern hemisphere. Hence most of the eggs from one season's grazing remain unhatched on the ground during the winter and usually only one generation is possible each year for the bulk of this species. However, some *N. battus* eggs deposited in the spring are capable of hatching in the autumn of the same year, resulting in significant numbers of L_3 on the pasture at this time. The ingested L_3 penetrate the mucosa of the small intestine and moult to the L_4 stage around the fourth day. After moulting to the L_5, the parasites inhabit the lumen, sometimes superficially coiled around villi. The prepatent period is 14–16 days.

Nematodirus filicollis

Description: The adults are long slender worms, males measuring 10–15 mm and females 15–24 mm in length. A small but distinct cephalic vesicle is present. The male has two sets of parallel rays in each of the main bursal lobes (Fig. 1.35). The spicules are long and slender with fused tips and terminate in a narrow pointed swelling (Table 1.10b). The female has a truncate blunt tail with a small spine (similar to *N. spathiger*), and the egg is

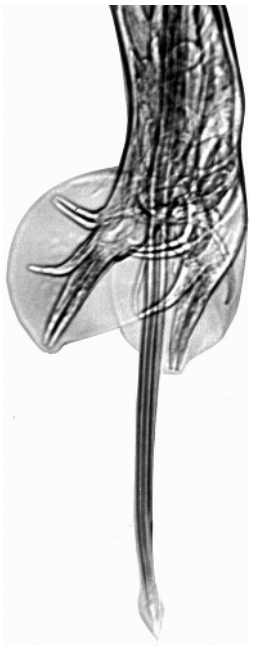


Fig. 1.35 Male bursa and spicules of *Nematodirus filicollis* with two sets of parallel rays in the dorsal lobes.

large, ovoid (130–200 × 70–90 µm), thin-shelled and colourless and twice the size of the typical trichostrongyle egg (see Fig. 4.4).

Life cycle: Development to the L_3 takes place within the eggshell. *Nematodirus filicollis* does not have the same critical hatching requirements as *N. battus*. Hatching occurs over a more prolonged period and so larvae often appear on the pasture within 2–3 months of the eggs being excreted in the faeces. The parasitic phase within the host is similar to that of *N. battus*. The prepatent period is 2–3 weeks.

Nematodirus spathiger

Description: The adults are slender worms, males measuring around 10–15 mm and females 15–25 mm in length. A small but distinct cephalic vesicle is present. The male has two sets of parallel rays in each of the main bursal lobes. The spicules are long and slender with fused tips and terminate in a spoon-shaped tip (Table 1.10c). The female has a truncate blunt tail with a small spine (similar to *N. filicollis*), and the egg is large, ovoid, thin-shelled and colourless and twice the size of the typical trichostrongyle egg. The egg measures 175–260 by 106–110 µm and usually contains an embryo of eight cells when passed in the faeces. Infective larvae measure around 1100 µm and have eight gut cells (see Fig. 4.15).

Life cycle: As for *N. fillicollis*.

Nematodirus helvetianus

Description: Adult males measure around 11–16 mm and females 17–24 mm in length. The male has two sets of parallel rays in each of the main bursal lobes and the dorsal lobe is not separated from the lateral lobe. The long slender spicules terminate in a fused point, with the surrounding membrane being lanceolate (Table 1.10d). The female has a truncate tail with a small spine. The egg is large (160–233 by 87–121 µm), ovoid with slightly sharp poles and clear, and twice the size of the typical trichostrongyle egg. The chitinous eggshell is thin with a smooth surface and contains 2–8 large dark blastomeres, which are separated from the yolk membrane by quite a large fluid-filled cavity.

Life cycle: *Nematodirus helvetianus* does not have the same critical hatching requirements as *N. battus* and so the larvae often appear on the pasture within 2–3 weeks of the eggs being excreted in the faeces. More than one annual generation is therefore possible. The parasitic phase within the host is similar to that of *N. battus*. The prepatent period is around three weeks.

Nematodirus abnormalis

Description: Adult males measure around 11–17 mm and females 18–25 mm. The spicules are asymmetrical with the distal ends bent to form an asymmetrical lancet (Table 1.10e).

Nematodirus mauritanicus

Description: Adult females are 21–24 mm and males 13–15 mm long. Male spicules are joined for part of their length with the tips enclosed in a thin lanceolate membrane.

Nematodirus lamae

Description: These are small worms, females 14–20 mm, males 10–13 mm long. Male worms have a deeply emarginated dorsal lobe with two distinct lobules and long spicules, with the distal end enlarged and terminating in two distinct bifurcated medioventral processes.

Nematodirus leporis

Description: Male worms are 8–15 mm and female worms 16–20 mm in length. The bursa has rounded lobes with parallel posterolateral and mediolateral bursal rays and the spicules are long. The eggs are large (250 × 100 µm).

Nematodirella

Nematodirella spp. (Table 1.11) are narrow worms and are similar to *Nematodirus*. Male spicules are extremely long and thin.

Nematodirella dromedarii

Description: Males are 10–15 mm and females 10–30 mm in size. The very long spicules can measure up to half the body length and are equal in size (Fig. 1.36). Eggs are large, measuring about 250 by 125 µm.

Table 1.11 *Nematodirella* species.

Species	Hosts	Site
Nematodirella dromedarii	Camels (dromedaries)	Small intestine
Nematodirella cameli	Camels (Bactrians), elk, reindeer	Small intestine
Nematodirella alcides (syn. *Nematodirus longispiculata*, *Nematodirella longissimespiculata*)	Elk	Small intestine

Life cycle: This is thought to be similar to that of *Nematodirus* spp. (not *N. battus*).

Nematodirella cameli

Description: Males are 16–17 mm and females 21–25 mm in size. In the males, the spicules are asymmetrical, thin and extremely long, adjoining each other closely over their entire length, forming rounded swellings distally from which branch off spine-shaped distal extremities.

Nematodirella alcides

Synonyms: *Nematodirus longispiculata*, *Nematodirella longissimespiculata*

Description: Males are 15–17 mm and females 23–25 mm in size. The spicules are long, thin and filiform with a spear-like tip.

Lamanema

The main species is *Lamanema chavezi* which infects the small intestine of alpacas and vicunas.

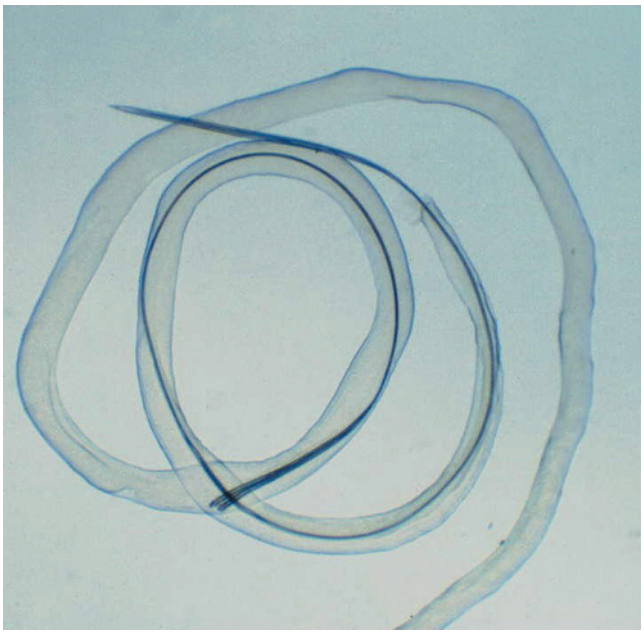


Fig. 1.36 *Nematodirella dromedarii* showing the very long male spicules.

Lamanema chavezi

Description: Small worms, females measuring 14–18 mm and males 9–11 mm long. There is a shallow buccal capsule with dorsal tooth and two small lateroventral teeth at the base. In the male, the lateral lobes are large, the dorsal lobe is small and there are short spicules and a large gubernaculum.

Life cycle: Ingested infective larvae penetrate the intestinal mucosa and migrate to the liver and lungs. Maturation is completed by migration of the worms back to the intestine via the trachea.

Ollulanus

These are very minute worms. Males are 0.7–0.8 mm and females 0.8–1 mm long. The buccal cavity is small. Microscopic identification is by the presence of the spiral coil of the head.

Life cycle: The worms are viviparous, the larvae developing to the L_3 stage in the uterus of the females. Autoinfection can occur, the shed L_3 developing into adult worms on the gastric mucosa in around 4–5 weeks. The whole life cycle may be completed endogenously and transmission, at least in the cat, is thought to be via ingestion of vomit containing the L_3. The worms live under a layer of mucus in the stomach wall and the anterior end of the worm is often located within the gastric crypts. The main species is *Ollulanus tricuspis* which infects the stomach of cats, wild felids, pigs, dogs and foxes.

Ollulanus tricuspis

Description: It is identified microscopically by the spiral coil of the head. The male bursa is well developed and the spicules are stout and each is split into two for a considerable portion of its length. The female has a tail, which terminates in three or four short cusps. The vulva is in the posterior part of the body and there is only one uterus and ovary.

FAMILY HELLIGMONELLIDAE

Nippostrongylus

The main species is *Nippostrongylus brasiliensis* (syn. *Nippostrongylus muris*, *Heligmosomum muris*) which infects the small intestine of rats, mice, hamsters, gerbils, rabbits and chinchillas.

Nippostrongylus brasiliensis

Synonyms: *Nippostrongylus muris*, *Heligmosomum muris*

Description: Adults are filiform and reddish in colour; males measure 2.1–4.5 mm and females 2.5–6 mm in length. They usually appear as a tight coil. The medium-sized eggs are ellipsoidal, thin-shelled with a smooth surface and measure about 52–63 by 28–35 µm. They contain a morula.

Life cycle: The life cycle is direct and typically trichostrongyloid. Infection is usually percutaneous and larvae migrate via the lungs.

Worms are adult by around five days post infection and are usually short-lived. The prepatent period is 5–6 days.

Nematospiroides

The main species is *Nematospiroides dubius* (syn. *Heligmosomoides polygyrus*) which infects the small intestine of rats and mice.

Nematospiroides dubius

Description: Adults are long red worms measuring 0.6–1.3 cm in length, with a coiled tail and a cephalic vesicle. The medium-sized eggs are ovoid with a thin smooth shell, measure around 68 by 43 µm and contain a morula.

Life cycle: Typically trichostrongyloid with infection via the L_3. The prepatent period is nine days and patency may last for up to eight months.

FAMILY DICTYOCAULIDAE

Dictyocaulus

Adults of *Dictyocaulus* spp. (Table 1.12) are slender thread-like worms, white/light grey in colour and up to 8–10 cm in length. Their location in the trachea and bronchi and their size are diagnostic. The buccal capsule and the bursa are small. The brown spicules are short and often have a slightly granular appearance. There is some debate over the species taxonomy in deer.

Life cycle: The female worms are ovoviviparous, producing eggs containing fully developed larvae, which hatch almost immediately. The L_1 migrate up the trachea, are swallowed and pass out in the faeces. The larvae are unique in that they are present in fresh faeces, are characteristically sluggish, and their intestinal cells are filled with dark-brown food granules (Fig. 1.37). In consequence, the preparasitic stages do not need to feed. Under optimal conditions, the L_3 stage is reached within five days but usually takes longer in the field. The L_3 leave the faecal pat to reach the herbage either by their own motility or through the agency of the ubiquitous fungus *Pilobolus*. After ingestion, the L_3 penetrate the intestinal mucosa and pass to the mesenteric lymph nodes where they moult. The L_4 then travel via the lymph and blood to the lungs, and break out of the capillaries into the alveoli about one week after infection. The final moult occurs in the bronchioles a few days later and the young adults then move up the bronchi and mature. See **life cycle 2**.

Table 1.12 *Dictyocaulus* species.

Species	Hosts	Site
Dictyocaulus viviparus	Cattle, buffalo, deer, camels	Trachea, lungs
Dictyocaulus filaria	Sheep, goats, camelids	Trachea, lungs
Dictyocaulus arnfieldi	Horses, donkeys, zebras	Trachea, lungs
Dictyocaulus eckerti (syn. *Dictyocaulus noerneri*)	Deer (roe deer, fallow deer, red deer), cattle	Trachea, lungs
Dictyocaulus capreolus	Deer (roe deer, moose)	Trachea, lungs

Fig. 1.37 First-stage larvae of *Dictyocaulus viviparus*. (Courtesy of Laura Rinaldi).

Dictyocaulus viviparus

Description: The adults are slender thread-like worms; males measure around 4–5.5 cm and females 6–8 cm in length. The buccal ring is triangular in shape. They are very similar to *D. filaria* but the posterolateral and mediolateral rays are entirely fused together. First-stage larvae present in fresh faeces are about 300–450 µm in length and 25 µm in width, the intestinal cells containing numerous brownish chromatin granules (see Fig. 1.37). The head is rounded, there being no protruding anterior knob (cf. *D. filaria* in sheep and goats). The oesophagus is simple strongyloid and the tail terminates in a blunt point.

Life cycle: The prepatent period is around 3–4 weeks in cattle. The prepatent period in red deer is 20–24 days.

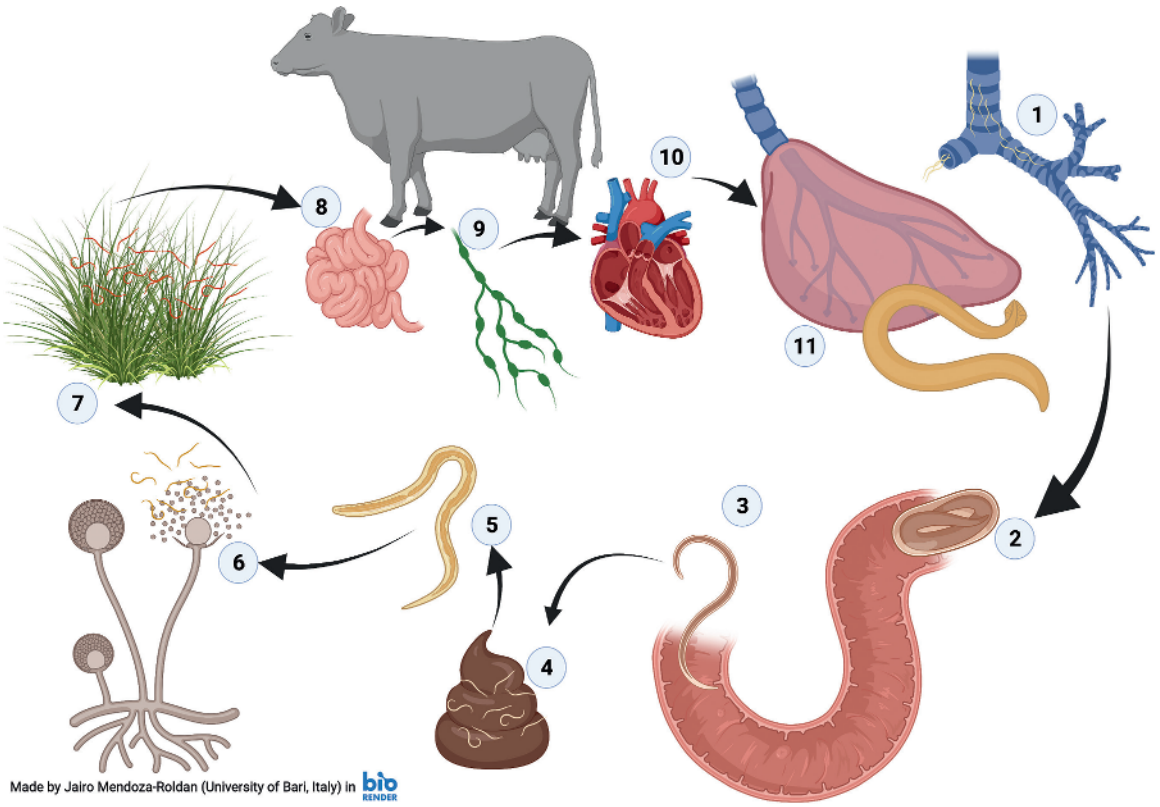
Dictyocaulus filaria

Description: The worms are white with the intestine visible as a dark band. Males measure around 4–8 cm and females 6–10 cm in length. In the bursa, the posterolateral and mediolateral rays are fused together, except at their extremities. The dark-brown spicules are stout and shaped like a boot. The vulva is located just posterior to the middle of the worm. The eggs measure 112–138 by 69–90 µm and contain fully formed first-stage larvae when laid. The L_1 resembles that of *D. viviparus* but has a characteristic small protruding cuticular knob at the anterior extremity (see Fig. 4.13b). The larva measures 550–580 µm in length, has a blunt tail (see Fig. 1.59a) and its intestinal cells contain numerous dark food granules.

Life cycle: The prepatent period is about 4–5 weeks.

LIFE CYCLE 2. LIFE CYCLE OF *DICTYOCAULUS VIVIPARUS*

Dictyocaulus viviparus causes bronchopulmonary disease in cattle. Adult parasites live in the trachea and large bronchi (1) and induce productive bronchitis with severe cellular infiltration (mainly eosinophils, neutrophils and macrophages) that may obstruct the alveolar lumen. The surface of infected lungs displays extended emphysematous areas, oedema and atelectasis. Adult females are ovoviviparous, and release eggs containing the L_1 (2) that, in most cases, hatch in the bronchi (3). The larvae migrate up the trachea and, once swallowed, are excreted with the faeces (4). In the environment, larvae develop into infective L_3 (5) within five days; these are poorly motile and in order to exit the faecal pat, they climb up the sporangium of *Pilobolus* fungi (6). When the sporangium discharges, the larvae are also discharged on the surrounding vegetation (7). Once ingested by the grazing hosts, the larvae penetrate the intestinal mucosa (8) and, via the lymphatic circulation, travel to the mesenteric lymph nodes (9) where they moult to L_4. The latter travel via the lymphatics and blood vessels (10) to the lungs (11) where they penetrate the alveoli. From here, within ~7 days, the immature adults reach the bronchi where they develop into sexually mature adults.



Dictyocaulus arnfieldi

Description: The adults are slender, thread-like and whitish in colour, the adult males measuring around 3.5 cm and the females 6.5 cm in length. Male worms have a small non-lobulated bursa with short rays, with the mediolateral and posterolateral rays fused for half their length. The spicules are short, of equal length and slightly curved. The medium-sized, ellipsoidal, thin-walled eggs measure 80–100 by 50–60 µm and are embryonated. First-stage larvae emerge from the egg very early and measure 290–480 µm, with a posterior transparent protuberance (Fig. 1.38). The contents are granular in appearance.

Life cycle: The detailed life cycle is not fully known, but is considered to be similar to that of the bovine lungworm, *D. viviparus*, except in the following respects. The adult worms are most often found in the small bronchi and their thin-shelled eggs, containing the first-stage larvae, are coughed up before they are swallowed, passed in the faeces and then hatch soon after being deposited. The prepatent period is around 2–3 months. Patent infections are common in donkeys of all ages, but in horses generally only occur in foals and yearlings. In older horses, the adult lungworms rarely attain sexual maturity.

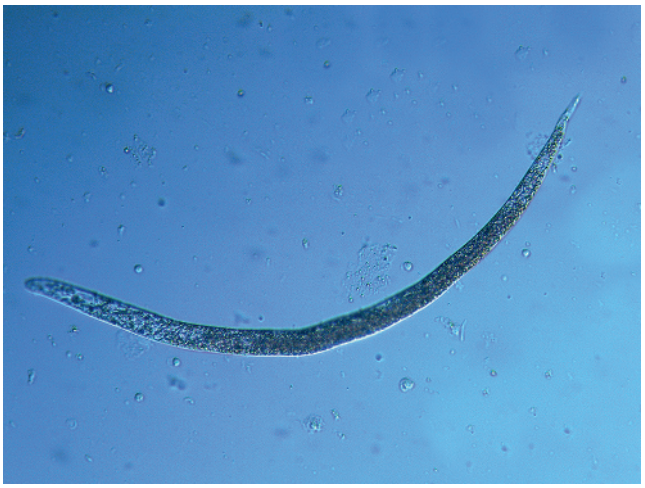


Fig. 1.38 *Dictyocaulus arnfieldi* first-stage larva showing the terminal protuberance.

Dictyocaulus eckerti

Synonym: *Dictyocaulus noerneri*

Description: Similar to *D. viviparus* but the mouth opening is elongate and the buccal ring is kidney-shaped.

Dictyocaulus capreolus

Description: Distinguished from *D. eckerti* on the basis of the morphology of the buccal capsule and the bursa.

SUPERFAMILY STRONGYLOIDEA

There are several important parasites of domestic mammals and birds in this superfamily of bursate nematodes. Most are characterised by a large buccal capsule, which often contains teeth or cutting plates, and in some there are prominent leaf crowns surrounding the mouth opening. The bursa of males is well developed and a gubernaculum or telamon is usually present. The spicules are usually of equal length. The adults occur on mucosal surfaces of the gastrointestinal and respiratory tracts and feeding is generally by the ingestion of plugs of mucosa.

With the exception of three genera, *Syngamus*, *Mammomonogamus* and *Cyathostoma*, which are parasitic in the trachea and major bronchi, and *Stephanurus* found in the perirenal area, all other genera of veterinary importance in this superfamily are found in the intestine and can be conveniently divided into two groups, the strongyles and hookworms.

The strongyles are parasitic in the large intestine and the important genera are *Strongylus*, *Triodontophorus* ('large strongyles' of horses), *Chabertia* and *Oesophagostomum*. Also in this group of small strongyles are the genera *Poteriostomum*, *Craterostomum* and *Oesophagodontus*.

The cyathostomins (cyathostomes or trichonemes) or 'small strongyles' of horses (subfamily Cyathostominae) include the genera *Cyathostomum*, *Cylicocyclus*, *Cylicodontophorus* and *Cylicostephanus* (formerly the single genus *Trichonema*).

Syngamus and *Cyathostoma* are important parasites of the respiratory tract of birds. *Mammomonogamus* are parasites of the respiratory tract of cattle, sheep and goats.

FAMILY STRONGYLIDAE

SUBFAMILY STRONGYLINAE

Strongylus

Members of this genus (Table 1.13) live in the large intestine of horses and donkeys. These are robust dark-red worms which are easily seen against the intestinal mucosa (Fig. 1.39). The well-developed deep buccal capsule of the adult parasite is prominent, as is the bursa of the male. The anterior margin of the buccal capsule usually bears leaf-like cuticular structures (leaf crowns or corona radiata). Species differentiation is based on size and the presence and shape of the teeth in the base of the buccal capsule. See **life cycle 3**.

Table 1.13 *Strongylus* species.

Species	Hosts	Site
Strongylus edentatus (syn. *Alfortia edentatus*)	Horses, donkeys	Large intestine
Strongylus equinus	Horses, donkeys	Large intestine
Strongylus vulgaris (syn. *Delafondia vulgaris*)	Horses, donkeys	Large intestine

Fig. 1.39 *Strongylus* spp. adult worms (large strongyles) on the intestinal mucosa with smaller cyathostomins (small strongyles) also present.

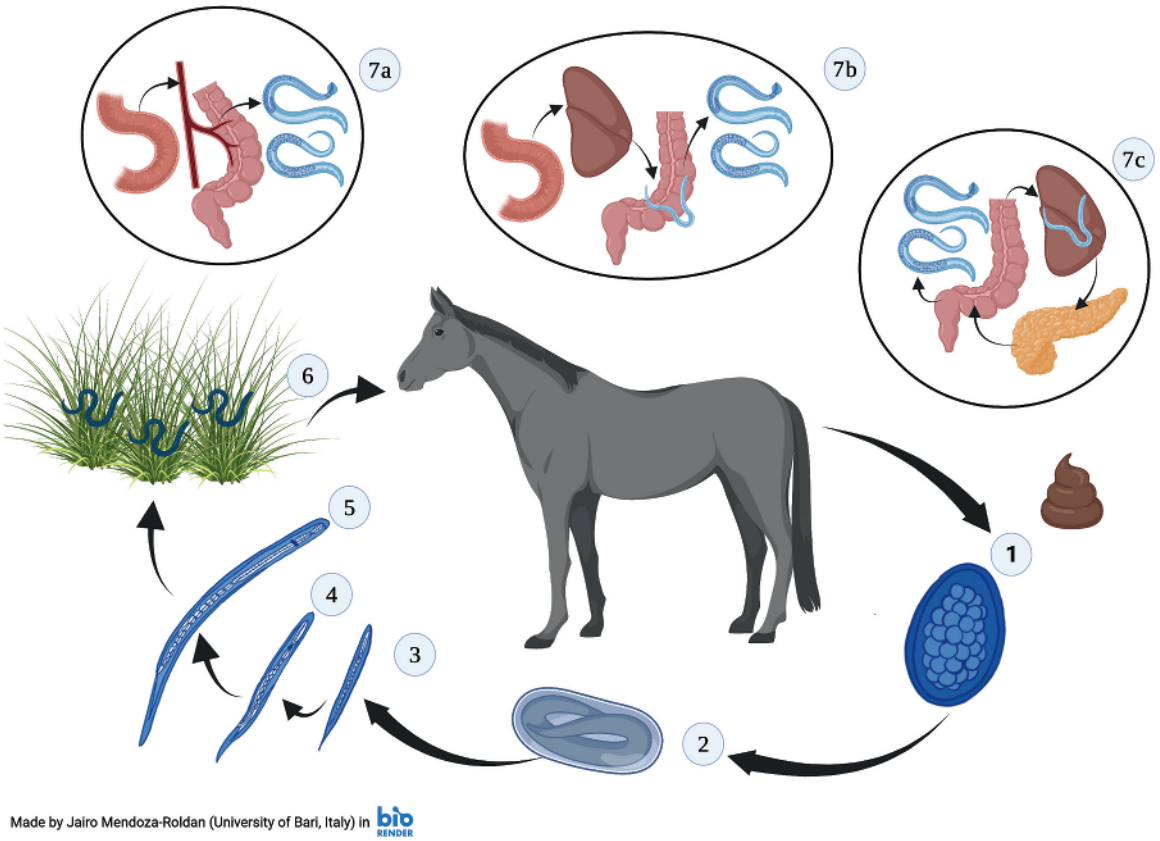
LIFE CYCLE 3. LIFE CYCLE OF *STRONGYLUS* SPP. (LARGE STRONGYLES OF EQUINES)

Adults of *Strongylus vulgaris*, *Strongylus edentatus* and *Strongylus equinus*, known as large strongyles, live in the lumen of the caecum and colon, where they attach to the mucosa with their buccal capsule. The infected horse sheds elliptical, unembryonated eggs in the faeces (1) into the environment (2). The rhabditiform first-stage larva hatches from the egg (3) and moults to second- (4) and third-stage larva (5), becoming infective within two weeks. Horses acquire the infection by ingesting infective L_3 contaminating the environment (6). After ingestion, depending on species, the larvae undergo different somatic migrations before establishing in the final site of infection.

Larvae of *S. vulgaris* (7a) penetrate the intestinal wall and, after a week, moult in the submucosa and penetrate the small arteries to reach the main branches of the cranial mesenteric artery and the ileo-caeco-colic system. Here, the larvae persist for many months and after a further moult, return to the intestinal wall via the blood vessels. As the larvae grow, nodules form within the caecal and colonic walls. These eventually rupture and release the immature adults in the intestinal lumen. Here, the worms reach sexual maturity and reproduce, thus completing the life cycle.

Larvae of *S. edentatus* (7b) penetrate the intestinal wall and travel to the liver parenchyma, where they moult to become fourth-stage larvae and migrate to the subserosa, in proximity to the hepatorenal ligament and parietal peritoneum, where they form haemorrhagic nodules. Here, the larvae moult to become pre-adults and return to the intestine, where they form purulent nodules containing the immature adults. The latter are subsequently released from the nodules and develop to sexually mature adults, completing the life cycle.

Larvae of *S. equinus* (7c) penetrate the caecal and colonic wall, where they form nodules within the muscular and subserosal layers. After moulting, the larvae migrate to the liver parenchyma, and subsequently to the pancreas and intestinal lumen, where the parasites complete development to sexually mature adults.



Strongylus edentatus

Description: Robust dark-red worms that are easily seen against the intestinal mucosa (Fig. 1.40). The well-developed buccal capsule of the adult parasite is prominent, as is the bursa of the male. Male are 2.3–2.8 cm and females 3.3–4.4 cm. The head end is wider than the rest of the body. Species differentiation is based on size and the presence and shape of the teeth in the base of the buccal capsule. The buccal capsule is wider anteriorly than at the middle and contains no teeth (Fig. 1.41a). The medium-sized eggs have almost similar poles and barrel-shaped side walls. They have a smooth thin shell, measure 78–88 by 48–52 µm and contain a morula with several large blastomeres.

Life cycle: Eggs, which resemble those of the trichostrongyles, are passed in the faeces and development from egg to the L_3 under

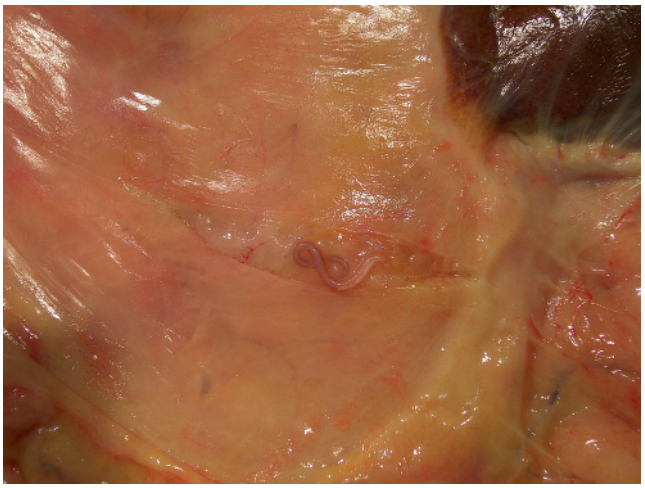


Fig. 1.40 *Strongylus edentatus* feeding on the mucosa of the large intestine. (Courtesy of Aránzazu Meana).

summer conditions in temperate climates requires approximately two weeks. Infection is by ingestion of the L_3. Subsequently, parasitic larval development of the three species of *Strongylus* differs and will be dealt with separately.

After penetration of the intestinal mucosa, L_3 travel via the portal system and reach the liver parenchyma within a few days. About two weeks later, the moult to L_4 takes place; further migration then occurs in the liver and by 6–8 weeks post infection, larvae can be found subperitoneally around the hepatorenal ligament. The larvae then travel under the peritoneum to many sites, with a predilection for the flanks and hepatic ligaments. The final moult occurs after four months and each L_5 then migrates, still subperitoneally, to the wall of the large intestine where a large purulent nodule is formed, which subsequently ruptures with release of the young adult parasite into the lumen. The prepatent period is usually about 10–12 months and is the longest of the strongyles.

Strongylus equinus

Description: Robust dark-red worms that are easily seen against the intestinal mucosa. The well-developed buccal capsule of the adult parasite is prominent, as is the bursa of the male. Males are 2.6–3.5 cm and females 3.8–4.7 cm. The head end is not marked off from the rest of the body. Species differentiation is based on size and the presence and shape of the teeth in the base of the buccal capsule. The buccal capsule is oval in outline and there are external and internal leaf crowns. At the base of the buccal capsule is a large dorsal tooth with a bifid tip and two smaller subventral teeth (Fig. 1.41b). The dorsal oesophageal gland opens into the buccal capsule through a number of pores situated in a thickened ridge, the dorsal gutter, formed by the wall of the buccal capsule. The male has two simple slender spicules. In the female, the vulva lies 12–14 mm from the posterior extremity. The eggs are similar to those of *S. edentatus* and measure 75–92 by 41–54 μm.

Life cycle: The adult parasites live in the caecum and colon. The free-living phase is as described for *S. edentatus*. Of the three *Strongylus* species, least is known of the larval migration of *S. equinus*. It appears that the L_3 lose their sheaths while penetrating the wall of the caecum and ventral colon and within one week provoke the formation of nodules in the muscular and subserosal layers of the intestine. The moult to L_4 occurs within these nodules and the larvae then travel across the peritoneal cavity to the liver where they migrate within the parenchyma for six weeks or more. After this time, L_4 and L_5 have been found in and around the pancreas before their appearance in the large intestinal lumen. The prepatent period is 8–9 months.

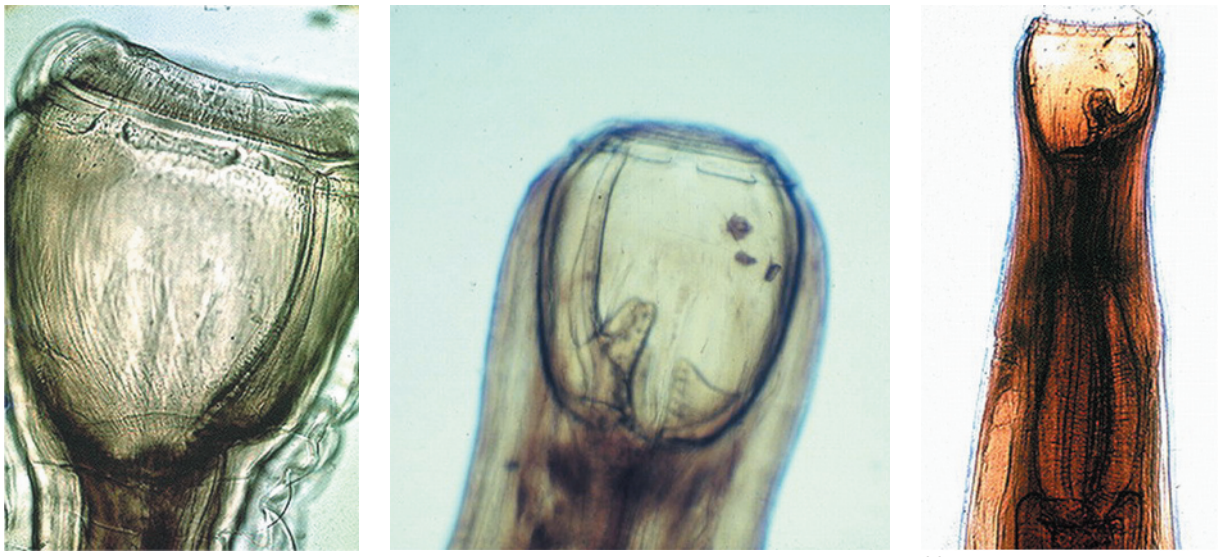


Fig. 1.41 (a) Anterior of *Strongylus edentatus* showing the cup-shaped buccal capsule, which is devoid of teeth. (b) Anterior of *Strongylus equinus* showing oval buccal capsule with a large dorsal tooth and smaller subventral conical teeth. (c) Anterior of *Strongylus vulgaris* showing ear-shaped rounded teeth at the base of the buccal capsule.

Strongylus vulgaris

Description: Adults of this species are shorter and thinner than the other two *Strongylus* species. Robust dark-red worms that are easily seen against the intestinal mucosa. The well-developed buccal capsule of the adult parasite is prominent, as is the bursa of the male. Males are 14–16 mm and females 20–24 mm. The head end is not marked off from the rest of the body. Species differentiation is based on size and the presence and shape of the teeth in the base of the buccal capsule. The buccal capsule is oval in outline and contains two ear-shaped teeth at its base (Fig. 1.41c). The elements of the leaf crowns are fringed at their distal extremities. The dorsal oesophageal gland opens into the buccal capsule through a number of pores situated in a thickened ridge, the dorsal gutter, formed by the wall of the buccal capsule. The thin-shelled eggs are similar to those of *S. edentatus* and measure 83–93 by 48–52 µm.

Life cycle: The free-living phase is as described for the other two species. Following ingestion, the L_3 penetrate the intestinal mucosa and moult to L_4 in the submucosa of the caecum and ventral colon seven days later. These then enter small arteries and arterioles and migrate on the endothelium to their predilection site in the cranial mesenteric artery and its main branches. After a period of development of several months, the larvae moult to L_5 and return to the intestinal wall via the arterial lumina. Nodules are formed around the larvae mainly in the wall of the caecum and colon when, due to their size, they can travel no further within the arteries, and subsequent rupture of these nodules releases the young adult parasites into the lumen of the intestine. The prepatent period is 6–7 months.

Triodontophorus

Members of the genus *Triodontophorus* (Table 1.14) are non-migratory, large strongyles frequently found in large numbers in the colon of horses and donkeys. They are reddish worms 1–2.5 cm in length, readily visible on the colonic mucosa. The buccal capsule is subglobular and thick-walled with three pairs of large oesophageal teeth, each composed of two plates, the anterior rim of which is thickened and surrounded by six plate-like structures (Fig. 1.42). The dorsal gutter is prominent. The spicules of the male terminate in small hooks.

Life cycle: Little information is available on the developmental cycle of this genus, but it is thought to be similar to that of cyathostomes.

Triodontophorus brevicauda

Description: Medium-sized worms, varying in size from around 9 to 25 mm. The buccal capsule is subglobular and thick-walled with three large oesophageal teeth composed of two plates which are smooth except for three elevations on each and protrude into the buccal capsule. The anterior rim of the buccal capsule is thickened anteriorly and surrounded by six plate-like structures. The submedian papillae are short, broad and conical. The external leaf crown consists of numerous slender elements protruding from the buccal collar, with an equal number of inner leaf crown elements. In the female, the vulva is close to the anus and the tail is very short. The large smooth egg is ovoid with almost similar poles and barrel-shaped side walls and contains a morula with very dark blastomeres. It measures 130–140 by 55–65 µm.

Table 1.14 *Triodontophorus* species.

Species	Hosts	Site
Triodontophorus brevicauda	Horses, donkeys	Large intestine
Triodontophorus minor	Horses, donkeys	Large intestine
Triodontophorus nipponicus	Horses, donkeys	Large intestine
Triodontophorus serratus	Horses, donkeys	Large intestine
Triodontophorus tenuicollis	Horses, donkeys	Large intestine

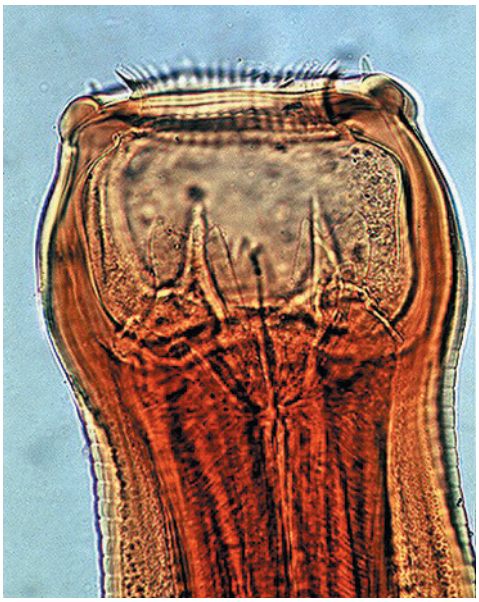


Fig. 1.42 Head of *Triodontophorus* spp. showing the location of teeth at the base of the buccal capsule.

Triodontophorus minor

Description: Medium-sized worms, varying in length from around 9 to 15 mm. The buccal capsule is subglobular and thick-walled with three large oesophageal teeth composed of two plates which are strongly denticulated and protrude into the buccal capsule. The anterior rim of the buccal capsule is thickened anteriorly and surrounded by six plate-like structures. The cuticle is strongly serrated in the cervical region. The external leaf crown consists of 44–50 slender elements protruding from the buccal collar, with an equal number of inner leaf crown elements. In the female, the vulva is close to the anus and the tail is short. The eggs are similar to those of *T. brevicauda*.

Triodontophorus nipponicus

Description: Medium-sized worms, varying in size from about 9 to 15 mm. The buccal capsule is subglobular and thick-walled with three large oesophageal teeth composed of two plates which are strongly denticulated, with three large denticulations, and protrude into the buccal capsule. The anterior rim of the buccal capsule is thickened anteriorly and surrounded by six plate-like structures. The cuticle is strongly serrated in the cervical region. The external

leaf crown consists of 56–69 slender elements protruding from the buccal collar, with an equal number of inner leaf crown elements. In the female, the vulva is close to the anus and the tail is short. The eggs are similar to those of *T. brevicauda*.

Triodontophorus serratus

Description: This is the largest species of the genus. Males measure 18–20 mm and females 20–26 mm in length. The buccal capsule is subglobular and thick-walled with three large oesophageal teeth composed of two plates that protrude into the buccal capsule. The anterior rim of the buccal capsule is thickened anteriorly and surrounded by six plate-like structures. The mouth collar appears as an inflated round tube around the mouth. The external leaf crown consists of numerous slender elements protruding from the buccal collar, with an equal number of inner leaf crown elements. In the female, the vulva is close to the anus and the tail is long. The eggs are similar to those of *T. brevicauda*.

Triodontophorus tenuicollis

Description: Males are around 17 mm and females 22 mm long. The buccal capsule is subglobular and thick-walled with three large oesophageal teeth composed of two plates which are finely denticulated and protrude into the buccal capsule. The anterior rim of the buccal capsule is thickened anteriorly and surrounded by six plate-like structures. The cuticle is strongly serrated in the cervical region; the dorsal lobe of the bursa is short and teeth are finely denticulated. The external leaf crown consists of numerous slender elements protruding from the buccal collar, with an equal number of inner leaf crown elements. In the female, the vulva is close to the anus. The eggs are similar to those of *T. brevicauda*.

Oesophagostomum

Worms of this genus (Table 1.15) are stout and whitish with a narrow cylindrical buccal capsule and measure 1–2 cm in length (Fig. 1.43). The body is often slightly curved. A ventral cervical groove is located near the anterior end of the worm and the anterior cuticle is dilated to form a cervical vesicle. Leaf crowns are present.

Life cycle: The preparasitic phase is typically strongyloid. The egg hatches on the ground, releasing the first-stage larva which moults to the second stage, and then to the infective third stage. Infection is by ingestion of L_3. There is no migration stage in the body, although there is limited evidence that skin penetration is possible. The larvae moult again and the fourth-stage larvae attach to, or enter, the wall of the intestine. These L_4 then emerge on to the mucosal surface, migrate to the colon and develop to the adult stage. The prepatent period is 5–7 weeks. On reinfection, the larvae may remain arrested as L_4 in nodules for up to one year.

Oesophagostomum columbianum

Description: Male worms are 12–17 mm and females 15–22 mm with large cervical alae, which induce a dorsal curvature of the anterior part of the body. The cuticle forms a high mouth collar shaped like a truncate cone. This is separated from the remainder of the body by a constriction. The cephalic vesicle is anterior to a cervical groove, behind which arise the cervical alae pierced by cervical papillae. External leaf crowns consist of 20–24 elements and the internal ones have two small elements to each external element. The male bursa is well developed with two alate spicules of equal length. The smooth, colourless, thin-shelled egg is a medium-sized (70–89 × 36–45 µm), regular broad ellipse with barrel-shaped walls and round wide poles, and contains 8–16 blastomeres when passed in the faeces (see Fig. 4.4). The L_3 have long filamentous tails, 32 gut cells and a rounded head and measure around 790 µm.

Life cycle: The prepatent period is about 45 days.

Table 1.15 *Oesophagostomum* species.

Species	Hosts	Site
Oesophagostomum columbianum	Sheep, goats, camels, wild ruminants	Large intestine
Oesophagostomum venulosum (syn. *Oesophagostomum virginimembrum*)	Sheep, goats, deer, camels	Large intestine
Oesophagostomum asperum	Sheep, goats	Large intestine
Oesophagostomum multifoliatum	Sheep, goats	Large intestine
Oesophagostomum radiatum	Cattle, water buffalo	Large intestine
Oesophagostomum dentatum	Pigs	Large intestine
Oesophagostomum brevicaudum	Pigs	Large intestine
Oesophagostomum longicaudatum	Pigs	Large intestine
Oesophagostomum quadrispinulatum	Pigs	Large intestine
Oesophagostomum georgianum	Pigs	Large intestine
Oesophagostomum granatensis	Pigs	Large intestine
Oesophagostomum apiostomum	Primates	Large intestine
Oesophagostomum bifurcum	Primates	Large intestine
Oesophagostomum aculateum	Primates	Large intestine
Oesophagostomum stephanostomum	Primates	Large intestine

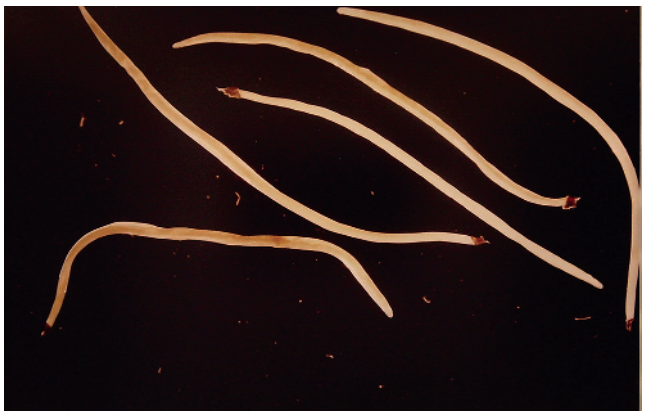


Fig. 1.43 Adult worms of *Oesophagostomum venulosum*.

Oesophagostomum venulosum

Synonym: *Oesophagostomum virginimembrum*

Description, gross: Males worms are 11–16 mm and females 13–24 mm long. Around the anterior oesophagus there is an inflated cuticular cephalic vesicle (Fig. 1.44). This terminates in a cervical groove, which is followed in some species by broad cervical alae. In the male the bursa is well developed. The head has a shallow buccal capsule with an external leaf crown of 18 elements. The external crown is compressed and so there is only a narrow opening into the buccal capsule. There are no lateral cervical alae and the worms are therefore not curved anteriorly. The cervical papillae are posterior to the oesophagus. The smooth, colourless, thin-shelled egg is a medium-sized (85–120 × 45–60 µm), regular broad ellipse with barrel-shaped walls, and contains 16–32 blastomeres when passed in the faeces. The L_3 have long filamentous tails, 32 gut cells and a rounded head.

Life cycle: The prepatent period is about 5–7 weeks.

Oesophagostomum multifolium

Description: Males measure 12–14 mm and females 14–17 mm in length.

Oesophagostomum radiatum

Description: Adult male worms are 12–17 mm and females 16–22 mm long. The cuticle forms a rounded mouth collar and large cephalic vesicle, constricted around the middle by a shallow annular groove (Fig. 1.45). External leaf crowns are missing and the internal ring consists of 38–40 small triangular denticles. Cervical papillae are present, just posterior to the cervical groove. The male bursa is well developed. The egg is a medium-sized (75–98 × 46–54 µm), regular, broad ellipse with barrel-shaped side walls and rounded poles, and contains 16–32 blastomeres when passed in the faeces. The colourless chitinous shell is thin with a smooth surface. Infective larvae (L_3) have long filamentous tails, 32 gut cells and a rounded head.

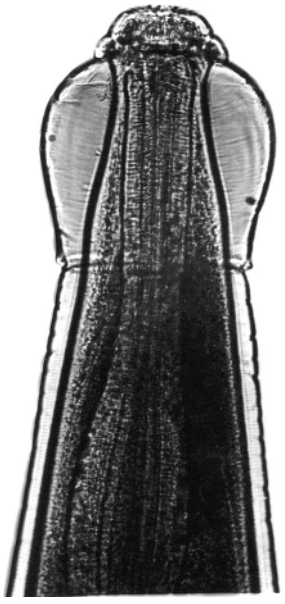


Fig. 1.44 Anterior of *Oesophagostomum venulosum* showing the large inflated cephalic vesicle.

Fig. 1.45 Anterior of *Oesophagostomum radiatum* showing the large cephalic vesicle.

Life cycle: The prepatent period is about 40 days.

Oesophagostomum dentatum

Description: Adult males are 8–10 mm and females 11–14 mm in length (Fig. 1.46). The cephalic vesicle is prominent but cervical alae are virtually absent. The nine elements of the leaf crown project forward and the internal leaf crown has 18 elements. The buccal capsule is shallow with parallel sides and the oesophagus is club-shaped with a narrow anterior end. In the female, the tail is

Fig. 1.46 *Oesophagostomum dentatum* adult worms.

relatively short. Eggs are ovoid, smooth with almost similar rounded poles and strongly barrel-shaped side walls. The shell is thin and colourless. They measure around 60–80 by 35–45 µm and contain 8–16 blastomeres in fresh faeces. L_3 are less than 600 µm with a tail less than 60 µm.

Oesophagostomum brevicaudum

Description: Males measure 6–7 mm and females 6.5–8.5 mm in length. There are 28–32 elements and 14–16 elements in the internal and external leaf crowns respectively. In the female, the tail is bent dorsally.

Oesophagostomum quadrispinulatum

Description: This worm is similar to *O. dentatum*, although the oesophagus is slightly more slender and the tail of the female is almost twice as long.

Poteriostomum

These worms (Table 1.16) measure about 9–21 mm in length. This genus is closely related to the genus *Cylicodontophorus*. The two genera are easily separated based on characteristics of the buccal capsule, especially the point of insertion of the internal leaf crowns, and on the character of the dorsal rays. The externodorsal ray and the dorsal ray of the bursa in this genus arise from a common trunk and the dorsal ray gives off, almost at 90°, two lateral branches near the origin of the externodorsal rays and the dorsal ray is cleft only to about half its length.

Poteriostomum imparidentatum

Description: Males are 9–14 mm and females 13–21 mm. This genus is closely related to the genus *Cylicodontophorus*. The two genera are easily separated based on characteristics of the buccal capsule, especially the point of insertion of the internal leaf crown and the character of the dorsal ray. In *P. imparidentatum* six elements of the internal leaf crown are markedly longer than the others.

Poteriostomum ratzii

Description: Males are 9–14 mm and females 13–21 mm. This genus is closely related to the genus *Cylicodontophorus*. The two genera are easily separated based on characteristics of the buccal capsule, especially the point of insertion of the internal leaf crown and the character of the dorsal ray. In *P. ratzii*, all elements of the internal leaf crown are of equal length.

Table 1.16 *Poteriostomum* species.

Species	Hosts	Site
Poteriostomum imparidentatum	Horses, donkeys	Large intestine
Poteriostomum ratzii	Horses, donkeys	Large intestine
Poteriostomum skrjabini	Horses, donkeys	Large intestine

Poteriostomum skrjabini

Description: Distinguished by a poorly defined dorsal gutter.

Craterostomum

These are relatively small worms, 6–11 mm long, and in general are similar to *Triodontophorus* (apart from the lack of protruding teeth and also the female vulva is located more anteriorly). The buccal capsule is of greatest diameter in the middle, with the wall thickened behind the anterior edge. The dorsal gutter is strongly developed. There is a shallow oesophageal funnel with three small triangular teeth that do not project into the buccal cavity. Elements of the external leaf crown are large and transparent and less numerous than the short broad elements of the inner leaf crown that ring the anterior ridge of the buccal capsule. Submedian papillae extend beyond the depressed mouth collar. In the female, the tail is long and pointed and the vulva is relatively far from the anus.

Craterostomum acuticaudatum

Description: The males measure about 6–10 mm and the females 7–11 mm in length. The internal leaf crown has 22–26 short elements and the external leaf crown bears 6–8 petal-shaped elements. The bottom of the buccal capsule is funnel-shaped and possesses a row of papillae which appear like a leaf crown. Teeth are absent from the buccal cavity. The buccal capsule is of greatest diameter in the middle, the wall being thickened behind the anterior edge. The dorsal gutter is strongly developed. The shallow oesophageal funnel has three small triangular teeth that do not project into the buccal cavity. Elements of the external leaf crown are large and transparent and less numerous than the short broad elements of the inner leaf crown that ring the anterior ridge of the buccal capsule. Submedian papillae extend beyond the depressed mouth collar. In the female, the tail is long and pointed and the vulva is relatively far from the anus.

Craterostomum tenuicauda

Description: Small worms, 6–10 mm long. The buccal capsule is of greatest diameter in the middle, the wall being thickened behind the anterior edge. The dorsal gutter is strongly developed. The shallow oesophageal funnel has three small triangular teeth that do not project into the buccal cavity. The elements of the external leaf crown (nine) are large and transparent and less numerous than the short broad elements of the inner leaf crown (18) that ring the anterior ridge of the buccal capsule. Submedian papillae are unnotched and extend beyond the depressed mouth collar. In the female, the tail is short and pointed and the vulva is relatively far from the anus.

Oesophagodontus

There is only one species in the genus. Male worms are 15–18 mm and females 19–24 mm in size. There is a slight constriction between the anterior region and the remainder of the body. The main species is *Oesophagodontus robustus* which infects the large intestine of horses and donkeys.

Oesophagodontus robustus

Description: Male worms are 15–18 mm and females 19–24 mm. There is a slight constriction between the anterior end and the rest of the body. The buccal capsule is shaped like a funnel with a thickened ring encircling its posterior margin. The oesophageal funnel has three lancet-like teeth that do not project into the buccal capsule. There is no dorsal gutter.

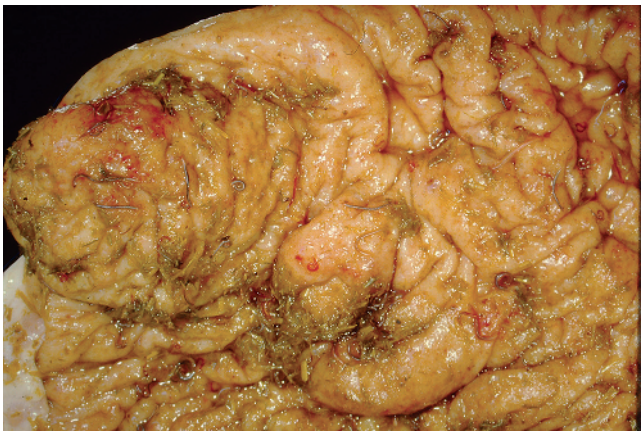


Fig. 1.47 Small strongyles (cyathostomins) on the mucosa of the ventral colon.

Codiostomum

The main species is *Codiostomum struthionis* which infects the large intestine and caecum of ostriches and rheas.

Codiostomum struthionis

Description: Adult worms are 13–17 mm in length. The large buccal capsule is subglobular with external and internal leaf crowns, but no teeth. The male bursa has a large projecting dorsal lobe. The third-stage larva has a rounded cephalic region and an acute termination of the tail, beyond which is a long filamentous sheath tail.

Life cycle: The life cycle is unknown but is considered to be direct.

SUBFAMILY CYATHOSTOMINAE

The 'small strongyles' include over 50 species, popularly known as trichonemes, cyathostomes or cyathostomins. For many years there has been a great deal of confusion in the classification of this group of parasites and in a new revision it has been proposed that the genus *Trichonema* be discarded and replaced by four main genera, namely *Cyathostomum*, *Cylicocyclus*, *Cylicodontophorus* and *Cylicostephanus*, these being collectively referred to as cyathostomes or, more recently, cyathostomins.

Small strongyles are small (5–12 mm long) bursate nematodes ranging in colour from white to dark red, the majority being visible on close inspection of the large intestinal mucosa or contents (Fig. 1.47). The well-developed short buccal capsule is cylindrical, without teeth, and species differentiation is based on characteristics of the buccal capsule and the internal and external leaf crowns.

Life cycle: Hatching of eggs and development to L_3 are complete within two weeks during the summer in temperate areas, after which the larvae migrate from the faeces on to the surrounding herbage. After ingestion, the L_3 exsheath and invade the wall of the ileum and large intestine where they develop to L_4 before emerging into the gut lumen and moulting to become young adult worms. The prepatent periods of members of this genus are generally between two and three months, although this may be extended due to hypobiosis in some species. See **life cycle 4**.

Cyathostomum

Cyathostomum spp. (Table 1.17) are small (5–12 mm in length) bursate nematodes ranging in colour from white to dark red, the majority being visible on close inspection of the large intestinal mucosa or contents. These parasites have a moderately high mouth collar, with cephalic papillae not very prominent. The well-developed short buccal capsule is cylindrical, without teeth, and species differentiation is based on characteristics of the buccal capsule and the internal and external leaf crowns. The buccal capsule is broader than deep and has no dorsal gutter. Elements of the external leaf crown are larger, broader and fewer than elements of the internal leaf crown. The inner leaf crown is deep in the buccal capsule and has sclerotised extrachitinous supports at or near the anterior edge of the buccal capsule (Fig. 1.48a). The dorsal ray of the male bursa is split to the origin of the externodorsal rays and the spicules are filiform, equal in length with 'pick'-shaped tips. In the female, the vulva is close to the anus. The tail may be straight or bent dorsally with a ventral bulge, anterior to the vulva. The eggs are medium-sized, a long ellipse, measuring about 100–110 by 40–45 µm. The shells are smooth and thin with almost similar poles and parallel side walls and contain a morula with several large blastomeres. It is not possible to distinguish between the eggs of the different species of cyathostomes.

LIFE CYCLE 4. LIFE CYCLE OF CYATHOSTOMINAE (SMALL STRONGYLES OF EQUINES)

Adult stages of small strongyles live in the lumen of the large intestine of the horse (1) that sheds unembryonated eggs with the faeces (2). After embryonation and first-stage larva formation (3) in the external environment, the egg hatches, releasing the first-stage larva, which moults twice to become an infective, third-stage larva (4) in about one week. The horse acquires the infection by ingesting infective larvae while grazing (5) or drinking contaminated water. After ingestion, the larvae migrate to the ileal, caecal and colonic glands (depending on genera and species of Cyathostominae), where they become encysted, thus forming nodules within the intestinal and submucosal wall (6). Within the nodules, the larvae continue their development and subsequently emerge within the intestinal lumen where they become adults. Adult males are characterised by a copulatory bursa with chitinous rays (7), whilst in females the location of the vulva and the morphology of the caudal end differ depending on genera (8). The morphology of the buccal capsule, with its external and internal chitinous crowns, is also taxonomically important and differs depending on species (9).

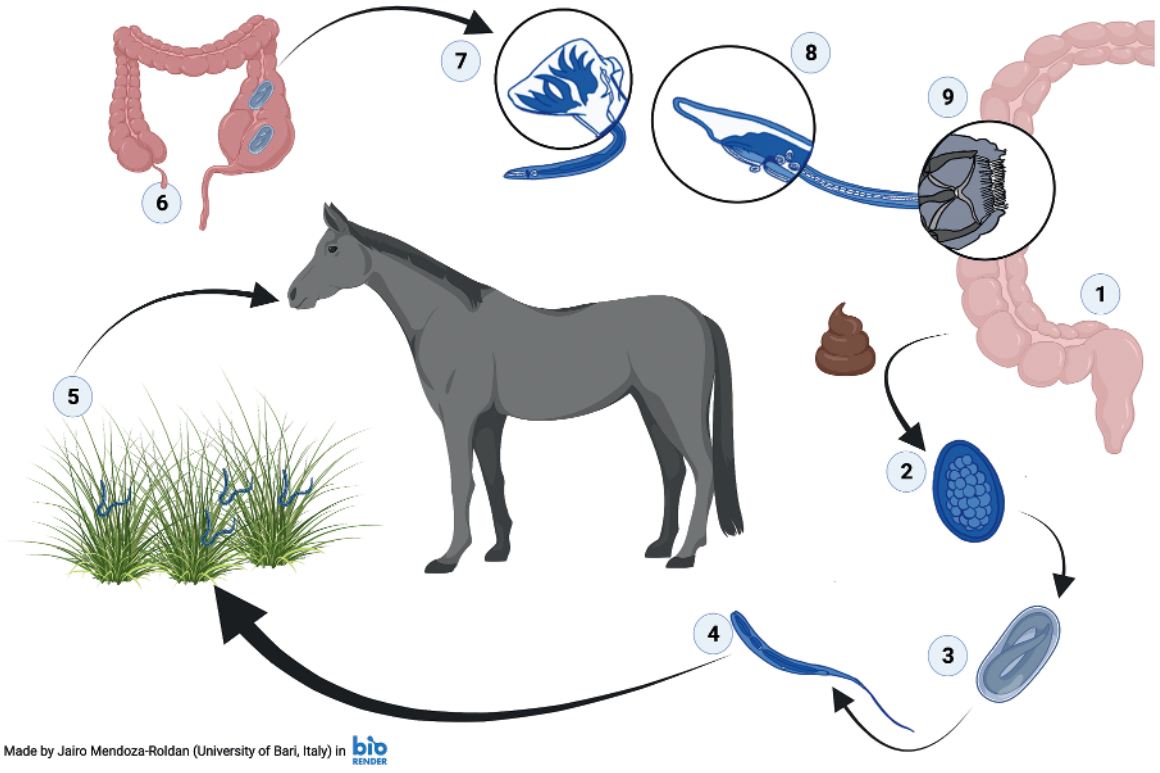


Table 1.17 *Cyathostomum* species.

Species	Hosts	Site
Cyathostomum alveatum (syn. *Cylichnostomum alveatum*, *Cylicostomum alveatum*, *Trichonema alveatum*, *Cylicocercus alveatus*)	Horses, donkeys	Large intestine
Cyathostomum catinatum (syn. *Cylichnostomum catinatum*, *Cylicostomum catinatum*, *Trichonema catinatum*, *Cylicocercus catinatum*)	Horses, donkeys	Large intestine
Cyathostomum coronatum (syn. *Cylichnostomum coronatum*, *Cylicostomum coronatum*, *Trichonema coronatum*, *Cylicostomias coronatum*)	Horses, donkeys	Large intestine
Cyathostomum labiatum (syn. *Cyathostomum labratum*, *Cylichnostomum labiatum*, *Cylicostomum labiatum*, *Trichonema labiatum*, *Cylicostomias labiatum*)	Horses, donkeys	Large intestine
Cyathostomum labratum (syn. *Cylichnostomum labratum*, *Cylicostomum labratum*, *Trichonema labratum*, *Cylicostomias labratum*)	Horses, donkeys	Large intestine
Cyathostomum montgomeryi (syn. *Cylicostomum montgomeryi*, *Trichonema labratum*, *Cylicotoichus montgomeryi*)	Horses, donkeys	Large intestine
Cyathostomum pateratum (syn. *Cylicodontophorus pateratum*, *Cylicostomum pateratum*, *Trichonema pateratum*, *Cylicostocercus pateratum*)	Horses, donkeys	Large intestine
Cyathostomum saginatum (syn. *Cylicostomum sagittatum*, *Trichonema sagittatum*, *Cylicostomias sagittatum*, *Cylicodontophorus sagittatum*)	Horses, donkeys	Large intestine
Cyathostomum tetracanthum (syn. *Strongylus tetracanthus*, *Sclerostomum tetracanthum*, *Cylichnostomum tetracanthum*, *Cylicostomum tetracanthum*, *Trichonema tetracanthum*, *Trichonema arcuata*, *Trichonema aegypticum*, *Cylicostomum aegypticum*)	Horses, donkeys	Large intestine

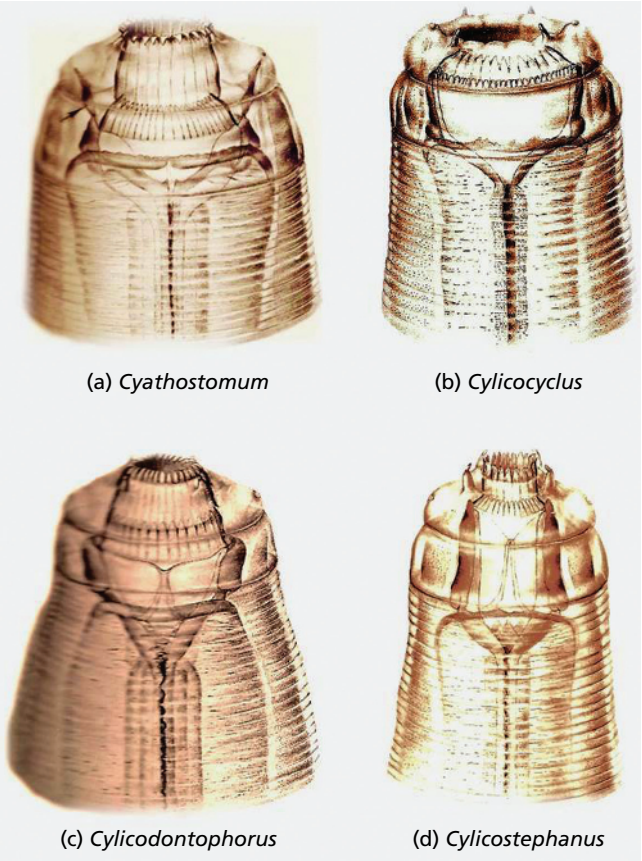


Fig. 1.48 Cystostomins showing characteristic features of the heads and buccal capsules used in generic and species identification: (a) *Cyathostomum*; (b) *Cylicocyclus*; (c) *Cylicodontophorus*; (d) *Cylicostephanus*. (Redrawn from Lichtenfels, 1975. Reproduced with permission from the Helminthological Society of Washington.)

Cyathostomum alveatum

Description: The walls of the buccal capsule have a uniform thickness posterior to the inner leaf crown, which is about one-third the depth of the buccal capsule.

Cyathostomum catinatum

Description: The inner leaf crown is more anterior on the lateral sides of the buccal capsule compared with the dorsal and ventral sides, but not in a sinuous line.

Cyathostomum coronatum

Description: Extrachitinous supports are prominent and the inner leaf crown forms an even line around the buccal cavity, which is as deep as it is broad and with walls that are thick and bent inwards.

Cyathostomum labiatum

Description: The mouth collar is notched and forms four distinct lips; the inner leaf crown elements are half the length of the external leaf crowns. Chitinous supports are spindle-shaped. The excretory pore is sited near the junction of the mid to posterior third of the oesophagus.

Cyathostomum labratum

Description: The mouth collar is not notched; the inner leaf crown elements are greater than half the length of the external leaf crowns. Chitinous supports are pyriform-shaped and the excretory pore is located near the middle of the oesophagus.

Cyathostomum montgomeryi

Description: Similar to *C. labiatum* but without well-defined lips. The wall of the buccal capsule is longer in dorsoventral view.

Cyathostomum pateratum

Description: The inner leaf crown is in a sinuous line deep in the buccal cavity (seen in lateral view).

Cyathostomum saginatum

Description: Similar to *C. coranatum* but the buccal capsule is shallow.

Cyathostomum tetracanthum

Description: The extrachitinous supports are nearly as large as the wall of the buccal capsule and appear as extensions of the buccal capsule wall.

Cylicocyclus

These parasites (Table 1.18) are small to medium-sized (10–25 mm in length) bursate nematodes ranging in colour from white to dark red, the majority being visible on close inspection of the large intestinal mucosa or contents. The well-developed short buccal capsule is cylindrical, without teeth, and species differentiation is based on characteristics of the buccal capsule and the internal and external leaf crowns. *Cylicocyclus* have a high mouth collar with broad lateral papillae. Elements of the external leaf crown are larger, fewer and broader than those of the inner leaf crown, the latter being short, with thin rods at or near the anterior edge of the buccal capsule. The buccal capsule is short, broader than deep, with thin walls tapering anteriorly, with a hoop-shaped thickening around the posterior margin. A dorsal gutter is usually absent from the buccal capsule (Fig. 1.48b). In the male the dorsal ray is split to the origin of the externodorsal rays and the spicules are filiform, of equal length with pick-shaped tails. In females, the vulva is near the anus and the tail is usually straight but may be bent slightly dorsally.

Table 1.18 *Cylicocyclus* species.

Species	Hosts	Site
Cylicocyclus adersi (syn. *Cylicostomum adersi*, *Trichonema adersi*)	Horses, donkeys	Large intestine
Cylicocyclus auriculatus (syn. *Cylichnostomum auriculatum*, *Cylicostomum auriculatum*, *Trichonema auriculatum*, *Cyathostomum auriculatum*)	Horses, donkeys	Large intestine
Cylicocyclus brevicapsulatus (syn. *Cylicostomum brevispiculatum*, *Cylichobrachytus brevispiculatum*, *Trichonema brevispiculatum*)	Horses, donkeys	Large intestine
Cylicocyclus elongatus (syn. *Cyathostomum elongatum*, *Cylichnostomum elongatum*, *Trichonema elongatum*, *Cylicoostomum elongatum*)	Horses, donkeys	Large intestine
Cylicocyclus insigne (syn. *Cylichnostomum insigne*, *Cylicostomum insdigne*, *Cylicostomum zebra*, *Trichonema insigne*)	Horses, donkeys	Large intestine
Cylicocyclus largocapsulatus (syn. *Trichonema largocapsulatus*)	Horses, donkeys	Large intestine
Cylicocyclus leptostomus (syn. *Cylichnostomum leptostomum*, *Trichonema leptostomum*, *Schultzitrichonema leptostomum*, *Cylicotetrapedon leptostomum*)	Horses, donkeys	Large intestine
Cylicocyclus maturmurai (syn. *Trichonema maturmurai*)	Horses, donkeys	Large intestine
Cylicocyclus nassatus (syn. *Cyathostomum nassatum*, *Cylichnostomum nassatum*, *Cylicostomum nassatum*, *Trichonema nassatum*, *Cylicocyclus bulbiferus*)	Horses, donkeys	Large intestine
Cylicocyclus radiatus (syn. *Cyathostomum radiatum*, *Cylichnostomum radiatum*, *Trichonema radiatum*, *Cylicostomum prionodes*)	Horses, donkeys	Large intestine
Cyliococyclus triramosus (syn. *Cylicostomum triramosum*, *Trichonema triramosum*)	Horses, donkeys	Large intestine
Cylicocyclus ultrajectinus (syn. *Cylicostomum ultrajectinum*, *Trichonema ultrajectinum*)	Horses, donkeys	Large intestine

Cylicocyclus adersi

Description: Buccal capsule is not shallow and the walls are of uniform thickness. The dorsal gutter is short but well developed. The inner leaf crown elements are few and wider than the external leaf crown elements and are of uniform length.

Cylicocyclus auriculatus

Description: The buccal capsule is not shallow and the dorsal gutter is absent. Lateral papillae are long ear-like or horn-like extending much higher than the mouth collar. The excretory pore and cervical papillae are located behind the oesophago-intestinal junction.

Cylicocyclus brevicapsulatus

Description: The buccal capsule is extremely shallow with delicate inconspicuous walls.

Cylicocyclus elongatus

Description: The buccal capsule is not shallow, the dorsal gutter is absent and the lateral papillae are not long. The excretory pore and cervical papillae are anterior to the oesophago-intestinal junction. The oesophageal funnel is nearly as large as the buccal capsule, and the oesophagus is greatly elongated with the posterior half enlarged and cylindrical.

Cylicocyclus insigne

Description: The buccal capsule is not shallow, the dorsal gutter is absent and the lateral papillae are not long. The excretory pore and the cervical papillae are anterior to the oesophago-intestinal junction. The external leaf crown elements are narrow; the inner leaf crown elements are much shorter than the external leaf crown elements and are of uniform length.

Cylicocyclus largocapsulatus

Description: The oesophago-intestinal valve is not elongate, the buccal capsule is large and the elements of the external leaf crown are about half as long as the buccal capsule is deep.

Cylicocyclus leptostomus

Description: The oesophago-intestinal valve is elongate, the buccal capsule is small and elements of the external leaf crown are almost as long as the buccal capsule is deep.

Cylicocyclus maturmurai

Description: The buccal capsule is not shallow and the walls are of uniform thickness. The inner leaf crown elements outnumber the external leaf crown elements and are of uniform length.

Cylicocyclus nassatus

Description: The buccal capsule is not shallow, with both lateral papillae and external leaf crown extending beyond the mouth collar. A dorsal gutter is present extending half of the depth of the buccal capsule. Submedian papillae are long and extend beyond the mouth collar. The external leaf crown has 20 elements. The buccal capsule has an internal shelf-like cuticular projection.

Cylicocyclus radiatus

Description: The oesophago-intestinal valve is not elongate, the buccal capsule is large and the elements of the external leaf crown are almost about one-third as long as the buccal capsule is deep.

Cyliococyclus triramosus

Description: The buccal capsule is not shallow, with both lateral papillae and the external leaf crown extending beyond the mouth collar. The dorsal gutter is short and button-like. The submedian papillae are short and do not extend beyond the mouth collar. The external leaf crown has 30 elements. The buccal capsule is without an internal projection.

Cylicocyclus ultrajectinus

Description: The buccal capsule is not shallow, the dorsal gutter is absent and the lateral papillae are not long. The excretory pore and cervical papillae are located near the oesophago-intestinal junction. The external leaf crown elements are broad; the inner leaf crown elements are as long, or longer, than the external leaf crown elements.

Cylicodontophorus

Small (7–14 mm in length) bursate nematodes (Table 1.19) ranging in colour from white to dark red, the majority being visible on close inspection of the large intestinal mucosa or contents. The well-developed short buccal capsule is cylindrical, without teeth, and species differentiation is based on characteristics of the buccal capsule and the internal and external leaf crowns. *Cylicodontophorus* have a high mouth collar, with inconspicuous lateral papillae and short and conical submedian papillae. The buccal capsule is short, thick-walled, of nearly uniform thickness and broader than deep. Inner leaf crown elements are longer, broader and less numerous than the external leaf crown elements, and are inserted near the anterior edge of the buccal capsule (Fig. 1.48c). The dorsal ray of the male bursa is split only to the proximal branch, and the spicules are filiform, equal in length with 'hook'-shaped tips. In the female, the tail is short with a sharp tip, and a prominent ventral bulge may be present anterior to the vulva.

Cylicodontophorus bicoronatus

Description: The dorsal gutter is well developed. The elements of the external and internal leaf crowns are nearly equal in size.

Cylicodontophorus euproctus

Description: The dorsal gutter is absent. The elements of the internal leaf crowns are twice as long as the elements of the external leaf crown. The oesophageal funnel is not well developed.

Cylicodontophorus mettami

Description: The dorsal gutter is absent. The elements of the internal leaf crowns are less than twice as long as the elements of the external leaf crown. The oesophageal funnel is well developed.

Table 1.19 *Cylicodontophorus* species.

Species	Hosts	Site
Cylicodontophorus bicoronatus (syn. *Cyathostomum bicoranatum*, *Cylichnostomum bicoronatum*, *Cylicostomum bicoranatum*, *Trichonema bicoranatum*)	Horses, donkeys	Large intestine
Cylicodontophorus euproctus (syn. *Cylichnostomum euproctus*, *Cylicostomum euproctus*, *Trichonema euproctus*)	Horses, donkeys	Large intestine
Cylicodontophorus mettami (syn. *Cylicostoma mettami*, *Cylicostomum mettami*, *Trichonema mettami*, *Cylicocercus mettami*, *Cylicostomum ihlei*)	Horses, donkeys	Large intestine

Cylicostephanus

These are small (4–10 mm in length) bursate nematodes (Table 1.20) ranging in colour from white to dark red, the majority being visible on close inspection of the large intestinal mucosa or contents. The well-developed short buccal capsule is cylindrical, without teeth, and species differentiation is based on characteristics of the buccal capsule and the internal and external leaf crowns. *Cylicostephanus* have a depressed mouth collar, with inconspicuous lateral papillae and prominent submedian papillae. The buccal capsule is slightly narrow anteriorly, with a wall of varying thickness and with a dorsal gutter. External leaf crown elements are longer, broader and less numerous than the internal leaf crown elements, which are short thin rods inserted near the anterior edge of the buccal capsule (Fig. 1.48d). The dorsal ray of the male bursa is split only to the proximal branch, and the spicules are filiform, equal in length with pick-shaped tips. In the female, the vulva is near the anus and the tail is usually straight.

Cylicostephanus asymetricus

Description: The walls of the buccal capsule are markedly thicker anteriorly, the elements of the external leaf crown are as broad as long, and the dorsal gutter extends almost to the base of the inner

Table 1.20 *Cylicostephanus* species.

Species	Hosts	Site
Cylicostephanus asymetricus (syn. *Cylicostomum asymetricum*, *Cylicotrapedon asymetricum*, *Schulzitrichonema asymetricum*)	Horses, donkeys	Large intestine
Cylicostephanus bidentatus (syn. *Cylicostomum bidentatum*, *Cylicotrapedon bidentatum*, *Trichonema bidentatum*, *Schulzitrichonema bidentatum*)	Horses, donkeys	Large intestine
Cylicostephanus calicatus (syn. *Cyathostomum calicatum*, *Cylichnostomum calicatum*, *Cylicostomum calicatum*, *Trichonema calicatum*, *Cylicostomum barbatum*, *Trichonema tsengi*)	Horses, donkeys	Large intestine
Cylicostephanus goldi (syn. *Cylichnostomum goldi*, *Cylicostomum goldi*, *Trichonema goldi*, *Schulzitrichonema goldi*, *Cylicostomum tridentatum*)	Horses, donkeys	Large intestine
Cylicostephanus hybridus (syn. *Cylicostomum hybridus*, *Trichonema hybridum*, *Schulzitrichonema hybridum*, *Trichonema parvibursatus*)	Horses, donkeys	Large intestine
Cylicostephanus longibursatus (syn. *Cylicostomum longibursatum*, *Trichonema longibursatum*, *Cylicostomum nanum*, *Cylicostomum calicatiforme*)	Horses, donkeys	Large intestine
Cylicostephanus minutus (syn. *Cylicostomum minutum*, *Trichonema minutum*)	Horses, donkeys	Large intestine
Cylicostephanus ornatus (syn. *Cylicostomum ornatum*, *Trichonema ornatum*, *Cylicostomias ornatum*, *Cyathostomum ornatum*, *Cylicodontophorus ornatum*)	Horses, donkeys	Large intestine
Cylicostephanus poculatus (syn. *Cyathostomum poculatum*, *Cylichnostomum poculatum*, *Cylicostomum poculatum*, *Trichonema poculatum*, *Petrovina poculatum*)	Horses, donkeys	Large intestine
Cylicostephanus skrjabini (syn. *Trichonema skrjabini*, *Petrovinema skrjabini*)	Horses, donkeys	Large intestine

leaf crown. The buccal capsule is asymmetrical in lateral view and the walls of the capsule are concave. The teeth in the oesophageal funnel are not prominent.

Cylicocyclus bidentatus

Description: The walls of the buccal capsule are markedly thicker anteriorly, the elements of the external leaf crown are as broad as long, and the dorsal gutter extends almost to the base of the inner leaf crown. The buccal capsule is asymmetrical in lateral view and the walls of the capsule are concave. The teeth in the oesophageal funnel are not prominent.

Cylicostephanus calicatus

Description: The buccal capsule is as broad as deep and the wall is of uniform thickness. The external leaf crowns are composed of 8–18 triangular elements and the submedian papillae are notched near their tips.

Cylicostephanus goldi

Description: The walls of the buccal capsule are of uniform thickness, the elements of the external leaf crown are twice as numerous as the elements of the inner leaf crown, and the dorsal gutter is button-like. The walls of the buccal capsule have a slight compound curve, being slightly thicker posteriorly. The female tail is bent dorsally. There are no prominent teeth in the oesophageal funnel.

Cylicostephanus hybridus

Description: The walls of the buccal capsule are of uniform thickness, the elements of the external leaf crown are twice as long as broad, and the dorsal gutter extends halfway to the base of the inner leaf crown. The walls of the buccal capsule are straight, slightly thicker posteriorly in dorsal view.

Cylicostephanus longibursatus

Description: The walls of the buccal capsule are of uniform thickness, the elements of the external leaf crown are twice as long as broad, and the dorsal gutter is button-like. The walls of the buccal capsule have a slight compound curve and are slightly thicker posteriorly.

Cylicostephanus minutus

Description: The buccal capsule is as broad as deep and the walls are of uniform thickness. The external leaf crowns are composed of 8–18 triangular elements and the submedian papillae are notched midway.

Cylicostephanus ornatus

Description: The walls of the buccal capsule are markedly thicker anteriorly, the elements of the external leaf crown are as broad as long, and the dorsal gutter extends almost to the base of the inner leaf crown. The buccal capsule is asymmetrical in lateral view and the walls of the capsule are concave. The teeth in the oesophageal funnel are not prominent.

Cylicostephanus poculatus

Description: The buccal capsule is deeper than broader in lateral view and the walls are much thicker posteriorly. The external leaf crown is composed of approximately 36 elements.

Cylicostephanus skrjabini

Description: The buccal capsule is deeper than broader in lateral view and the walls are much thicker posteriorly. The external leaf crown is composed of approximately 36 elements. It lacks a lateral projection on the inner wall of the buccal capsule and has a rim of dentiform processes at the bottom of the buccal capsule.

FAMILY CHABERTIDAE

Chabertia

Worms of this genus are usually found in low numbers in the majority of sheep and goats. The adults are 1.5–2 cm in length and are the largest nematodes found in the colon of ruminants. They are white with a markedly truncated and enlarged anterior end due to the presence of the very large buccal capsule. The anterior is curved slightly ventrally (Fig. 1.49).

Life cycle: The life cycle is direct. Eggs are passed in the faeces and hatch on the ground, releasing the first-stage larva which moults to the second stage, and then to the infective third stage. The host is infected by ingestion of the larva with the herbage. In the parasitic phase, the L_3 enter the mucosa of the small intestine and occasionally that of the caecum and colon; after a week they moult, the L_4 emerge on to the mucosal surface and migrate to congregate in the caecum where development to the L_5 is completed about 25 days

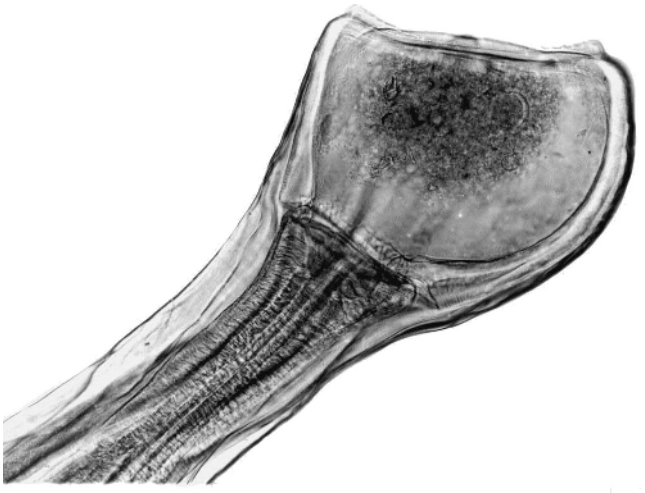


Fig. 1.49 Head of *Chabertia ovina* illustrating the large bell-shaped buccal capsule.

after infection. The young adults then travel to the colon. There is no migration stage in the body. The prepatent period is about 6–7 weeks. The main species is *Chabertia ovina* which infects the large intestine of sheep, goats and occasionally cattle.

Chabertia ovina

Description: The adults range from about 1.3 to 2 cm in length and are the largest nematodes found in the colon of ruminants. They are white and stout with a markedly truncated and enlarged anterior end due to the presence of the very large buccal capsule (Fig. 1.49). The huge buccal capsule, which is bell-shaped, has a double row of small papillae around the rim. There are no teeth. There is a shallow ventral cervical groove and anterior to it a slightly inflated cephalic vesicle. In the male, the bursa is well developed and the spicules are 1.3–1.7 mm long, with a gubernaculum. In the female, the vulva opens about 0.4 mm from the posterior extremity. The egg is a thin-shelled, smooth, medium-sized (90–100 × 45–55 µm), regular broad ellipse with wide slightly flattened poles (see Fig. 4.4). It contains 16–32 blastomeres. Infective larvae have a rounded head, 32 gut cells and a long filamentous tail and measure around 730 µm.

Agriostomum

Worms are stout and greyish-white in colour. Males are around 9–11 mm and females 13–16 mm in length. The main species is *Agriostomum vryburgi* which infects the small intestine of cattle, buffalo, oxen and zebu.

Agriostomum vryburgi

Description: The shallow buccal capsule opens anterodorsally and contains four pairs of large teeth on its margin and has a rudimentary leaf crown. The large wide oesophageal opening at the base of the buccal capsule houses two small subventral lancets. The bursa is well developed and the ventral rays are close together and parallel. A gubernaculum is present and the spicules are equal in length. Eggs measure about 130–190 by 60–90 µm.

FAMILY SYNGAMIDAE

Syngamus

The large reddish female and the small whitish male are permanently *in copula* forming a 'Y' shape (Fig. 1.50). They are the only parasites found in the trachea of domestic birds. Males possess two spicules.

Life cycle: Eggs escape under the bursa of the male and are carried up the trachea in the excess mucus produced in response to infection; they are then swallowed and passed in the faeces. Unlike other strongyloids, the L_3 develops within the egg. Infection may occur by one of three ways: first by ingestion of the L_3 in the egg, second by ingestion of the hatched L_3, or third by ingestion of a transport (paratenic) host containing the L_3. The most common paratenic host is the common earthworm, but a variety of other invertebrates including slugs, snails, beetles and some flies may act as transport hosts. After penetrating the intestine of the final host, the L_3 travel,

Fig. 1.50 *Syngamus trachea* male and female worms *in copula*. (Redrawn from Neumann, trans. Fleming, 1892).

via the liver, to the lungs, probably in the blood since they are found in the alveoli 4–6 hours after experimental infection. The two parasitic moults take place in the lungs within five days, by which time the parasites are 1–2 mm long. Copulation occurs around day 7 in the trachea or bronchi, after which the female grows rapidly. The prepatent period is 16–20 days. Longevity is around nine months. The main species is *Syngamus trachea* which infects the trachea of chickens, turkeys, gamebirds (pheasants, partridges, guinea fowl), pigeons and various wild birds.

Syngamus trachea

Synonyms: *Syngamus parvis*, *Syngamus gracilis*

Description: The large reddish female (around 1–3 cm) and the small whitish male (up to 0.5 cm) are permanently *in copula* forming a 'Y' shape (Fig. 1.50); they are the only parasites found in the trachea of domestic birds (Fig. 1.51). The worms have large, shallow, cup-shaped buccal capsules that have up to 10 teeth at their base.

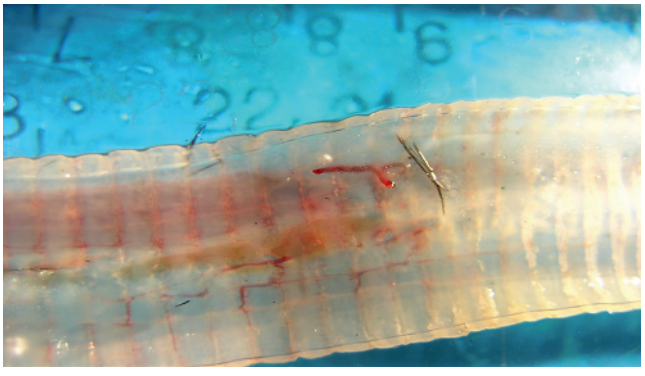


Fig. 1.51 *Syngamus trachea*: adult *in situ* (arrow). (Courtesy of Călin Mircea GHERMAN).

There are no leaf crowns. The bursal rays are short and thick and the two spicules are long and of simple form. The ellipsoidal thin-shelled eggs are 70–100 by 43–46 µm with a thick operculum at both ends. They are in the 16-cell stage when ejected.

Cyathostoma

The male bursa is well developed but worms in this species are not permanently *in copula*, as observed in *Syngamus*.

Life cycle: The life cycle is thought to be similar to that of *Syngamus*.

Cyathostoma bronchialis

Synonym: *Syngamus bronchialis*

Description: The worms are reddish in colour when fresh. Adult male worms are 4–6 mm and females much larger at 15–30 mm in length. The buccal capsule is large, deep and cup-shaped with 6–7 teeth at its base. The male bursa is well developed but worms in this species are not permanently *in copula*, as seen in *Syngamus trachea*. The medium-sized, lightly coloured eggs are ovoid with a smooth shell and possess a hardly perceptible operculum at one pole. They measure about 74–89 by 47–62 µm and the morula contains eight blastomeres.

Cyathostoma variegatum

Description: Adult worms are 0.4–3 cm long; males are 4–6 mm and females 16–31 mm. The buccal capsule is cup-shaped with 6–7 teeth at its base. The male bursa is well developed but worms in this species are not permanently *in copula*, which contrasts with the situation in *Syngamus trachea*. Eggs are 74–83 by 49–62 µm.

Mammomonogamus

These nematodes (Table 1.21) are similar to *Syngamus*. The worms are reddish in appearance and about 0.6–2 cm long. The females and males are found in permanent copulation. The large buccal capsule lacks a cuticular crown. There is a cervical papilla. Species of *Mammomonogamus* found in cats may be synonyms of the species found in ruminants.

Life cycle: The life cycle is direct but the mode of transmission is unknown.

Table 1.21 *Mammomonogamus* species.

Species	Hosts	Site
Mammomonogamus nasicola (syn. *Syngamus nasicola*, *Syngamus kingi*)	Sheep, goats, cattle, deer	Nasal cavities
Mammomonogamus laryngeus (syn. *Syngamus laryngeus*)	Cattle, buffalo, goats, sheep, deer, rarely humans	Larynx
Mammomonogamus auris (syn. *Syngamus auris*)	Cats	Ear canals
Mammomonogamus ierei (syn. *Syngamus ierei*)	Cats	Nasal cavities
Mammomonogamus mcgaughei (syn. *Syngamus mcgaughei*)	Cats	Nasal sinuses, pharynx

Mammomonogamus nasicola

Synonyms: *Syngamus nasicola*, *Syngamus kingi*

Description: The worms are reddish in appearance and about 1–2 cm long. Males are 4–6 mm and females 11–23 mm long and found in permanent copulation. The buccal capsule lacks a cuticular crown. Eggs are ellipsoid, 54–98 µm, with no operculum at either end.

Mammomonogamus laryngeus

Synonym: *Syngamus laryngeus*

Description: The worms are reddish in appearance and about 1–2 cm long. The females and males are found in permanent copulation. The buccal capsule lacks a cuticular crown. Eggs are ellipsoid, 42–45 by 75–85 µm, with no operculum at either end.

Mammomonogamus ierei

Synonym: *Syngamus ierei*

Description: Female worms are about 20 mm long, while male worms are 5–6.9 mm long and rather stocky in appearance. The worms are found with the bursa of the male attached at the level of the vulva of the female. There is a large buccal capsule that has eight large teeth at its base.

Stephanurus

Large worms found in the kidneys and perirenal tissues.

Life cycle: Preparasitic development from egg to L_3 is typically strongyloid, though earthworms may intervene as transport hosts. There are three modes of infection: by ingestion of the free L_3, ingestion of earthworms carrying the L_3, and percutaneously. After entering the body, there is an immediate moult and the L_4 travel to the liver in the bloodstream, either from the intestine by the portal stream or from the skin by the lungs and systemic circulation. In the liver, the final moult takes place and the young adults wander in the parenchyma for three months or more before piercing the capsule and migrating in the peritoneal cavity to the perirenal region. There they are enclosed in a cyst by the host reaction, and complete their development. The cyst communicates with the ureter either directly or, if it is more distant, by a fine connecting canal, allowing the worm eggs to be excreted in the urine. The prepatent period is 6–19 months and the worms have a longevity of about 2–3 years. The main species is *Stephanurus dentatus* which infects the kidney of pigs.

Stephanurus dentatus

Description: A large stout worm up to 4.5 cm long, with a prominent buccal capsule and transparent cuticle through which the internal organs may be seen. Males are 2–3 cm and females 3–4.5 cm long. The colour is usually pinkish. The size and site are diagnostic. The buccal capsule is cup-shaped with small leaf crowns and six external cuticular thickenings (epaulettes), of which the ventral and dorsal are most prominent, and six cusped teeth at the base. The male bursa is short and the two spicules of

either equal or unequal length. The medium-sized eggs are a broad ellipse with a thin transparent shell and appear only in the urine. They measure about 90–120 by 53–70 µm and contain numerous blastomeres (32–64).

FAMILY DELETROCEPHALIDAE

Deletrocephalus

The main species is *Deletrocephalus dimidiatus* which infects the small intestine of rheas.

Deletrocephalus dimidiatus

Description: Adult worms are stout and robust with a well-developed buccal capsule. Male worms are 9–11 mm and females 14–16 mm long. Males are bursate with long thin spicules. The eggs are 160 by 70 µm (Fig. 1.52). Third-stage larvae are approximately 720 µm long, with a rounded head, 28–31 intestinal cells and a short to medium tail.

Paradeletrocephalus

The main species is *Paradeletrocephalus minor* which infects the small intestine of rheas.

Paradeletrocephalus minor

Description: Adult worms are similar in size and appearance to *Deletrocephalus* spp. The buccal capsule has vertical ridges and there are no external, or internal, coronary rings.

SUPERFAMILY ANCYLOSTOMATOIDEA

Hookworms are parasites of the small intestine and the genera of veterinary importance are *Ancylostoma*, *Uncinaria*, *Bunostomum* and, to a lesser extent, *Gaigeria* and *Globocephalus*. In humans important hookworm genera are *Ancylostoma* and *Necator*.

FAMILY ANCYLOSTOMATIDAE

Ancylostoma

Ancylostoma spp. (Table 1.22) are reddish-grey worms, the colour depending on whether the worm has fed, and are readily recognised on the basis of size. The anterior extremity is usually bent dorsally. The worms have a well-developed buccal capsule, which is devoid of leaf crowns but is armed with teeth or chitinous cutting plates on its ventral edge.

Ancylostoma caninum

Description: The worms are reddish-grey in colour, depending on whether the worm has fed, and are readily recognised on the basis of size and by their characteristic hook-like posture (Fig. 1.53). Males are about 12 mm and females 15–20 mm in length (much smaller than the common ascarid nematodes, which are also found in the small intestine). The anterior end is bent dorsal and the oral aperture is directed anterodorsally. The buccal capsule is large with three pairs of sharp marginal teeth and a pair of ventrolateral teeth and possesses a dorsal gutter (Fig. 1.54). The male bursa is well developed. Eggs are typically 'strongylate' with slightly dissimilar bluntly rounded poles, barrel-shaped side walls and a thin smooth shell (see Fig. 4.7). They measure about 56–75 by 34–47 µm and contain 2–8 blastomeres when passed in faeces.

Life cycle: The life cycle is direct and, given optimal conditions, the eggs may hatch and develop to L_3 in as little as five days. Infection is

Table 1.22 *Ancylostoma* species.

Species	Hosts	Site
Ancylostoma braziliense	Dogs, foxes, cats, wild canids	Small intestine
Ancylostoma caninum	Dogs, foxes, wild canids, occasionally humans	Small intestine
Ancylostoma ceylanicum	Dogs, cats, wild felids, occasionally humans	Small intestine
Ancylostoma tubaeforme (syn. *Strongylus tubaeforme*)	Cats	Small intestine
Ancylostoma duodenale	Humans, primates	Small intestine

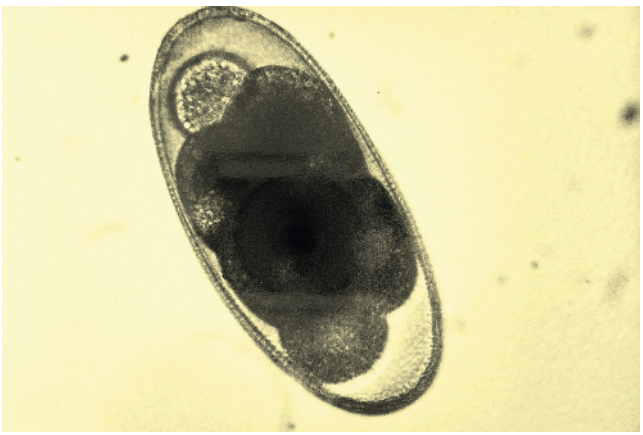


Fig. 1.52 *Deletrocephalus dimidiatus* egg.

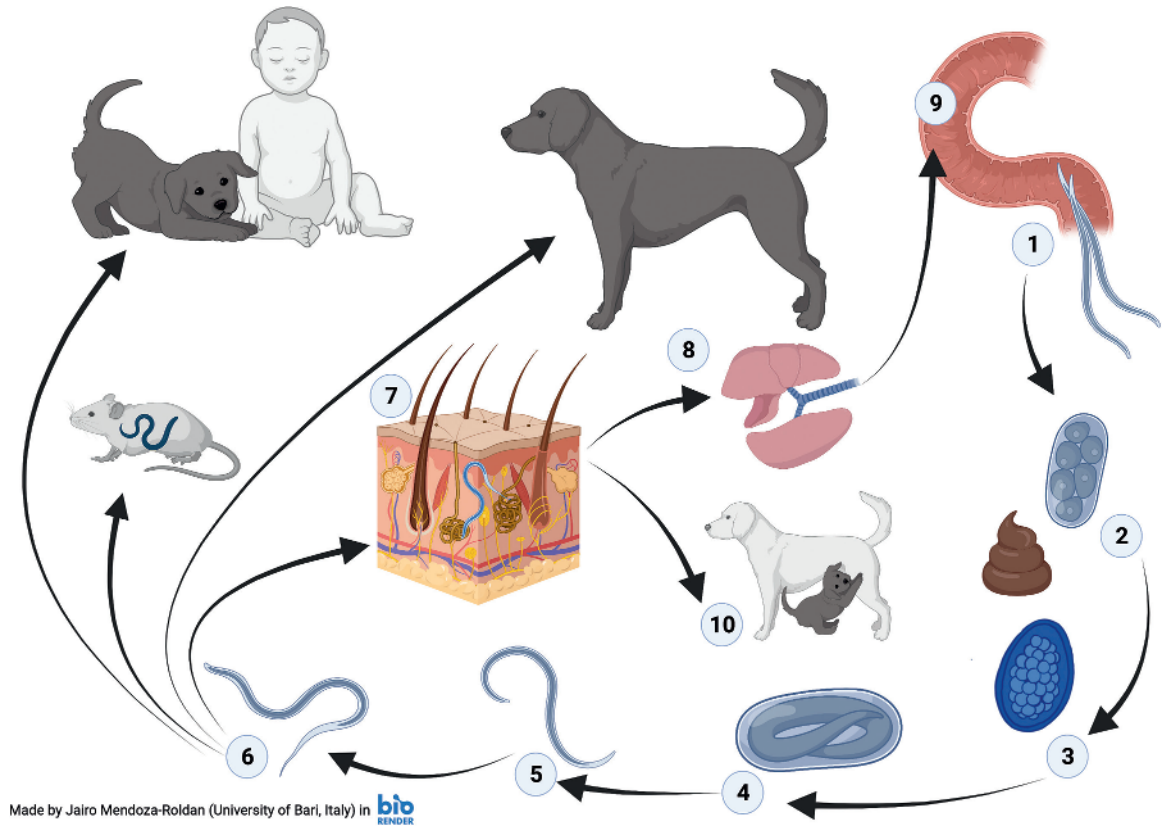
Fig. 1.53 *Ancylostoma caninum* adult worms.

Fig. 1.54 Head of *Ancylostoma caninum* showing the large buccal capsule containing pairs of teeth.

by skin penetration or ingestion, both methods being equally successful. Paratenic hosts can also be important. In percutaneous infection, larvae migrate via the bloodstream to the lungs where they moult to L_4 in the bronchi and trachea, and are then swallowed and pass to the small intestine where the final moult occurs. If infection is by ingestion, the larvae may either penetrate the buccal mucosa and undergo the pulmonary migration or pass directly to the intestine where the adult worms burrow their buccal capsules into the mucosa. Whichever route is taken, the prepatent period is 14–21 days. The worms are prolific egg layers and an infected dog may pass millions of eggs daily for several weeks. An important feature of *A. caninum* infection is that, in susceptible bitches, a proportion of the L_3 that reach the lungs migrate to the skeletal muscles where they remain dormant until the bitch is pregnant. They are then reactivated and, still as L_3, are passed in the milk of the bitch for a period of about three weeks after whelping. Transplacental transmission does not occur. See **life cycle 5**.

LIFE CYCLE 5. LIFE CYCLE OF *ANCYLOSTOMA CANINUM*

Adults of *Ancylostoma caninum* live in the lumen of the small intestine of the dog, that acts as definitive host (1). After mating, adult females release elliptical eggs, that contain 4–8 blastomeres (2). Once excreted in the environment with the host faeces, the egg develops (3) and after 24–48 hours, contains a rhabditoid first-stage larva (4). After hatching, within ~5 days, the larva moults to second- (5) and infective third-stage larva (L_3) (6). Infection occurs predominantly via percutaneous penetration or ingestion of the infective larvae. The larvae that penetrate the skin (7) migrate via the circulation to the lungs, where they moult and travel up the respiratory system (8), where they are coughed up and swallowed. Once swallowed, the larvae reach the small intestine and develop into adults (9). In infections that occur via ingestion of L_3 (directly or via paratenic hosts, that harbour infective larvae in their somatic tissues), these may reach the intestine immediately, there developing into adults, or penetrate the buccal mucosa and travel to the lungs and the upper respiratory system, where they are swallowed to reach the small intestine. A proportion of L_3 travel from the lungs to the skeletal muscles via the circulatory system; in the muscles, these larvae encyst to then become mobilised during pregnancy. These larvae are then excreted via the colostrum and milk and transmitted to the litter via the transmammary route (10) over the first three weeks from parturition. In humans, L_3 can penetrate the skin and cause cutaneous *larva migrans*.



Ancylostoma braziliense

Description: As for *A. caninum* except it is smaller than either *A. caninum* or *A. tubaeforme*. In the dog, males measure around 7.5 mm and females 9–10 mm in length. The buccal capsule is deep with two pairs of large dorsal and very small ventral teeth. Eggs are similar to those of *A. caninum*, measuring around 75–95 by 41–45 µm.

Life cycle: Similar in many respects to *A. caninum*, with both oral and percutaneous routes of infection, but transmammary transmission has not been demonstrated. Rodents can act as paratenic hosts. The prepatent period is about two weeks in the dog and cat.

Ancylostoma ceylanicum

Description: Almost identical to *A. braziliense*. The cuticular striations are wider than in *A. braziliense* and the inner pair of ventral teeth in the buccal capsule are larger.

Life cycle: Similar to *A. braziliense*. The prepatent period is about two weeks in the dog.

Ancylostoma tubaeforme

Synonym: *Strongylus tubaeforme*

Description: Almost identical to *A. caninum* but slightly smaller, the males measuring around 10 mm and the females 12–15 mm. The buccal capsule is deep with the dorsal gutter ending in a deep notch on the dorsal margin of the buccal capsule, the ventral margin of which bears three teeth on each side. The cuticle is thicker and the deep 'oesophageal' teeth are slightly larger than in *A. caninum*. The male bursa is well developed and the spicules are about 50% longer than in *A. caninum*. Eggs are similar to those of *A. caninum* and measure about 56–75 by 34–47 µm.

Life cycle: As for *A. braziliense*. The prepatent period is about three weeks.

Ancylostoma duodenale

Description: A small cylindrical worm, greyish-white in colour. There are two ventral plates on the anterior margin of the buccal capsule, each with two large teeth that are fused at their bases. A pair of small teeth is present in the depths of the buccal capsule. Males are 8–11 mm long with a copulatory bursa at the posterior end. Females are 10–13 mm long, with the vulva located at the posterior end. Eggs are typically 'strongylate' with slightly dissimilar bluntly rounded poles, barrel-shaped side walls and a thin smooth shell (Fig. 1.55).

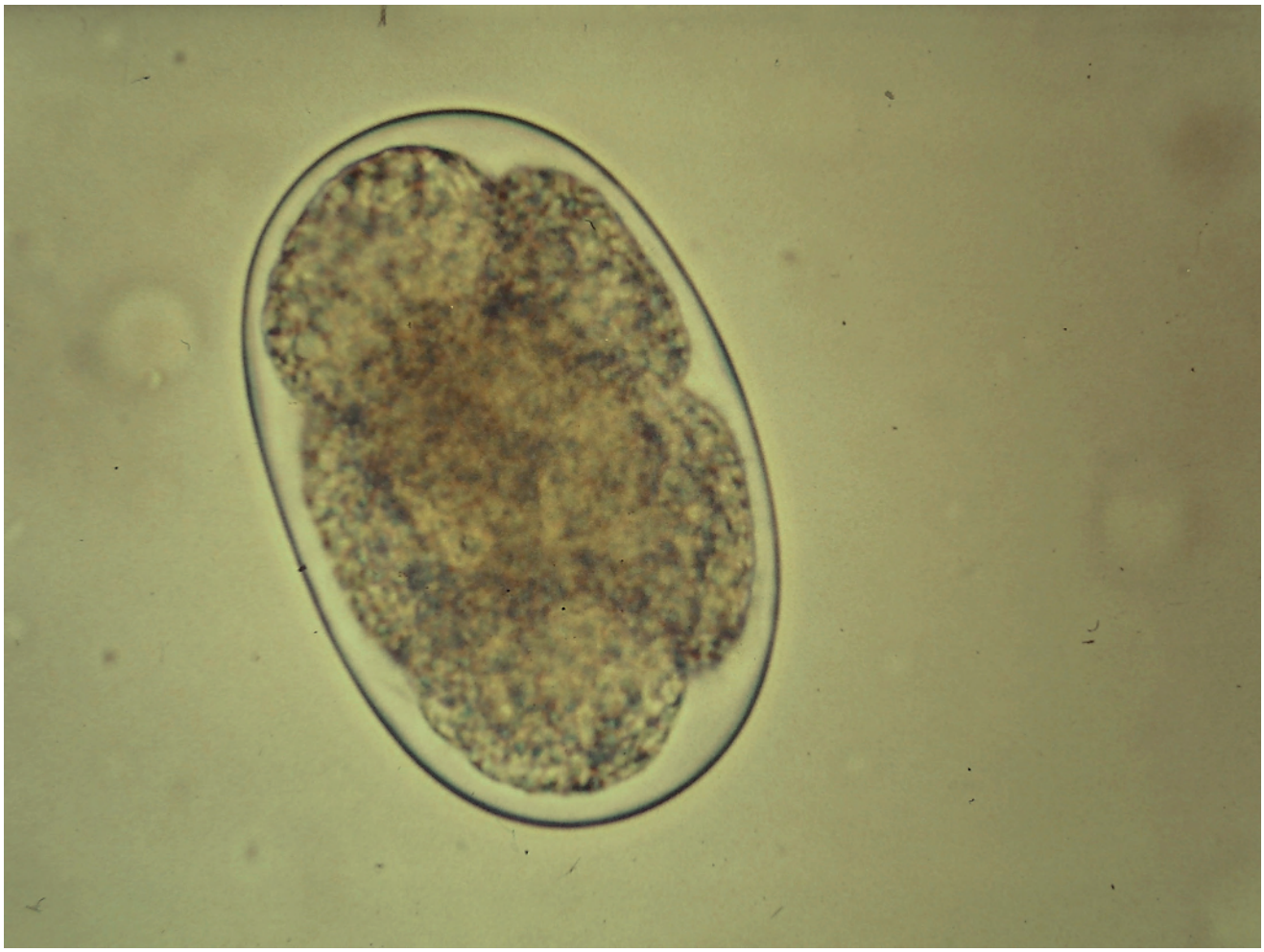


Fig. 1.55 Hookworm egg.

Life cycle: Similar to *A. caninum*. The prepatent period is about five weeks in the dog.

Uncinaria

The genus consists of a single species. The worms are small, up to about 1 cm long; males are 5–8.5 mm and females 7–12 mm long.

Life cycle: Infection with infective L_3 by oral infection, without pulmonary migration, is the usual route. Although the infective larvae can penetrate the skin, the infection rarely matures and there is no evidence as yet of transmammary or intrauterine transmission. Carnivores may become infected via the consumption of paratenic hosts, such as infected mice. The prepatent period is about 15 days. The main species is *Uncinaria stenocephala* which infects the small intestine of dogs, cats, foxes, other wild canids and felids.

Uncinaria stenocephala

Description: A small worm, up to about 1 cm long; males are 5–8.5 mm and females 7–12 mm. The adult worms have a large funnel-shaped buccal capsule, which has a pair of chitinous plates, lacks dorsal teeth, but has a pair of subventral teeth at the base (Fig. 1.56). The dorsal cone does not project into the buccal capsule. The male worm has a well-developed bursa with a short dorsal lobe and two large and separate lateral lobes and slender spicules. The eggs resemble those of *Ancylostoma caninum* but are slightly longer and wider and have a thicker shell. They are ovoidal with dissimilar poles and the thin smooth side walls are almost parallel. Eggs measure 65–80 by 40–50 µm and contain large blastomeres.

Necator

Male worms are usually 7–9 mm long and females about 9–11 mm in length. The main species is *Necator americanum* which infects the small intestine of humans, primates, dogs, cats and pigs.

Necator americanus

Description: Males are 7–9 mm and females about 9–11 mm long. The buccal capsule has two dorsal and two ventral cutting plates around the anterior margin. There is also a pair of subdorsal and a pair of subventral teeth located close to the rear of the buccal capsule.

Bunostomum

Bunostomum is one of the larger nematodes of the small intestine of ruminants (Fig. 1.57), being 1–3 cm long, stout, greyish-white and characteristically hooked at the anterior end, with the buccal capsule opening anterodorsally (Fig. 1.58). In the buccal capsule area there are cuticular festoons.

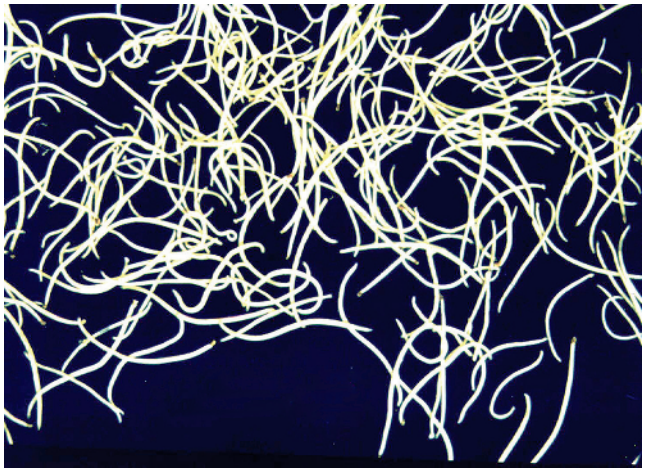


Fig. 1.57 Adult *Bunostomum phlebotomum*.

Fig. 1.56 Head of *Uncinaria stenocephala* showing the funnel-shaped buccal capsule and the pair of chitinous plates.

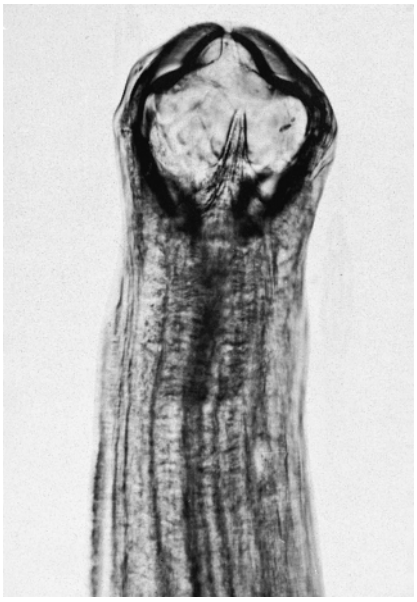


Fig. 1.58 Head of *Bunostomum phlebotomum* showing the large buccal capsule and cutting plates.

Life cycle: Infection with the L_3 may be percutaneous or oral. After skin penetration, the larvae travel to the lungs and moult to fourth-stage larvae before re-entering the gastrointestinal tract after approximately 11 days. Ingested larvae usually develop without a migration. Further development continues in the gut.

Bunostomum phlebotomum

Description: Male worms are 10–18 mm and female worms 24–28 mm in length. This species is very similar to *B. trigonocephalum* in sheep, but the dorsal cone is shorter and there are two pairs of small subventral lancets at its base. The large buccal capsule opens anterodorsally and bears on the ventral margin a pair of chitinous cutting plates and internally a large dorsal cone. Dorsal teeth are absent from the buccal capsule but there are two pairs of small subventral lancets at its base. In the male the bursa is well developed and has an asymmetrical dorsal lobe. The right externodorsal ray arises higher up on the dorsal stem and is longer than the left. It arises near the bifurcation of the dorsal ray, which divides into two tridigitate branches. The spicules are very long and slender. In the female the vulva opens a short distance in front of the middle of the body. The infective larva is small with 16 gut cells and a short filamentous tail. The egg is a medium-sized (97–106 by 45–55 µm), thin-shelled, irregular broad ellipse with blunt ends and dissimilar side walls, one being flattened. It contains four to eight darkly pigmented blastomeres.

Life cycle: The prepatent period is about 6 weeks after skin penetration, and 7–10 weeks after ingestion.

Bunostomum trigonocephalum

Synonym: *Monodontus trigonocephalum*

Description: Male worms are 12–17 mm and females 19–26 mm. The large buccal capsule opens anterodorsally and bears on the ventral margin a pair of chitinous cutting plates and internally a large dorsal cone. Dorsal teeth are absent from the buccal capsule but there are a pair of small subventral lancets at its base. In the male the bursa is well developed and the dorsal lobe is asymmetrical. The right externodorsal ray emerges higher up on the dorsal stem and is longer than the left. The left externodorsal ray arises near the bifurcation of the dorsal ray, which divides into two tridigitate branches. The spicules are slender, twisted and relatively short. In the female the vulva opens a short distance in front of the middle of the body. The infective larva is small with 16 gut cells and a short filamentous tail. The egg is medium-sized (75–104 × 45–57 µm), an irregular broad ellipse in shape, with similar wide poles and dissimilar side walls, one being flattened. The thin-shelled egg contains 4–8 darkly stained blastomeres.

Life cycle: The prepatent period is 4–8 weeks.

Gaigeria

The single species of this genus is a hookworm that occurs mainly in the duodenum of small ruminants.

Life cycle: The life cycle is thought to be direct; the main route of infection is percutaneous. Infective L_3 larvae resemble those of *Bunostomum trigonocephalum* and are susceptible to desiccation. The main species is *Gaigeria pachyscelis* which infects the duodenum and small intestine of sheep, goats and wild ruminants.

Gaigeria pachyscelis

Description: The worms are very similar in shape and size to *Bunostomum trigonocephalatum*. Adult male worms measure up to 2 cm and females up to 3 cm long. The buccal capsule contains a large dorsal cone and a pair of subventral lancets, which have several cusps each. There is no dorsal tooth. The male bursa has a large dorsal lobe and small lateral lobes, which are joined together ventrally. The anterolateral ray is short and rounded and is separated quite widely from the other lateral rays. The externodorsal rays arise from the main stem of the dorsal ray. The dorsal ray is split for about one-quarter of its length, and the two short branches terminate in three minute digitations. The spicules are short and stout and terminate with recurved unbarbed ends. The eggs measure 105–129 by 50–55 µm and their poles are bluntly rounded.

Globocephalus

Several species of this genus parasitise the small intestine of pigs. The worms are stout and whitish, and approximately 4–8 mm in length. The mouth opens subdorsally and the buccal capsule is globular in shape but with an absence of chitinous structures in the buccal capsule. There are no leaf crowns. The male bursa is well developed and possesses a gubernaculum and the spicules are slender.

Life cycle: The life cycle is direct, either by oral ingestion of L_3 larvae or by percutaneous penetration. Larval migration through the heart, lungs, trachea, oesophagus and stomach occurs. The main species is *Globocephalus urosubulatus* (syn. *Globocephalus longemucronatus*, *Globocephalus samoensis*) which infects the small intestine of pigs and wild boards.

Globocephalus urosubulatus

Synonyms: *Globocephalus longemucronatus*, *Globocephalus samoensis*

Description: A very small, stout, whitish worm. Males measure 4–7 mm and females 6–9 mm in length. The mouth opens subdorsally and the buccal capsule is globular. There are two raised cuticular rings near the opening of the mouth. There are small triangular chitinous plates in the buccal capsule. Leaf crowns are absent. The male bursa is well developed and the spicules are slender. Eggs are medium-sized, ovoid, smooth, with a thin colourless shell. They measure 50–60 by 26–35 µm and only have 6–8 blastomeres.

SUPERFAMILY DIAPHANOCEPHALOIDEA

FAMILY DIAPHANOCEPHALIDAE

Nematodes of the genus *Kalicephalus* are hookworms of snakes. The life cycle is direct with a prepatent period of 2–4 months.

SUPERFAMILY METASTRONGYLOIDEA

Most worms in this superfamily inhabit the lungs or the blood vessels adjacent to the lungs. The typical life cycle is indirect and the intermediate host is usually a mollusc.They may be conveniently

divided into four groups according to host: those occurring in **pigs** (Metastrongylidae: *Metastrongylus*); in **sheep** and **goats** (Protostrongylidae: *Muellerius*, *Protostrongylus*, *Cystocaulus*, *Spiculocaulus*, *Neostrongylus* and *Varestrongylus*); in **deer** (*Elaphostrongylus*, *Parelaphostrongylus*); and in the domestic and wild **carnivores** (Filaroididae: *Oslerus*, *Filaroides*, Angostrongylidae: *Angiostrongylus*, *Aelurostrongylus*; and Crenosomatidae: *Crenosoma*, *Troglostrongylus*).

FAMILY METASTRONGYLIDAE

Metastrongylus

Members of this genus (Table 1.23) are slender white worms, up to 6 cm in length, found in pigs. The site and long slender form are sufficient for generic identification. These worms have two lateral trilobed lips. Individual species are differentiated on the size and shape of the male spicules. The dorsal ray of the bursa is small. The life cycle involves an earthworm intermediate host. The ellipsoid eggs have rough thick shells, are 45–57 by 38–41 µm in size and are larvated when laid.

Life cycle: In cold temperatures the eggs are very resistant and can survive for over a year in soil. Normally, however, they hatch almost immediately, the intermediate host ingesting the L_1. In the earthworm, development to L_3 takes about 10 days at optimal temperatures of 22–26 °C. The longevity of the L_3 in the earthworm is similar to that of the intermediate host itself and may be up to seven years. The pig is infected by ingestion of earthworms and the L_3, released by digestion, travel to the mesenteric lymph nodes and moult. The L_4 then reach the lungs by the lymphatic–vascular route, the final moult occurring after arrival in the air passages.

Metastrongylus apri

Synonym: *Metastrongylus elongatus*

Description: The slender white adult male worms measure up to 25 mm and the females up to 58 mm in length. There are six small papillae located around the oral opening. The male bursa is relatively small and the dorsal rays are reduced. The spicules are filiform, around 4 mm long, and each terminates in a single hook. The vulva of the female is near the anus and both are covered in cuticular swellings. Eggs measure around 50–63 by 33–42 µm and contain a fully developed first-stage larva when laid.

Life cycle: The prepatent period is about 24 days.

Table 1.23 *Metastrongylus* species.

Species	Hosts	Site	Intermediate hosts
Metastrongylus apri (syn. *Metastrongylus elongatus*)	Pigs, wild boar	Lung	Earthworms (*Lumbricus*, *Dendrobaena*, *Eisena*, *Helodrilus* spp.)
Metastrongylus pudendotectus (syn. *Metastrongylus brevivaginatus*)	Pigs, wild boar	Lung	Earthworms (*Lumbricus*, *Dendrobaena*, *Eisena*, *Helodrilus* spp.)
Metastrongylus salmi	Pigs, wild boar	Lung	Earthworms (*Lumbricus*, *Dendrobaena*, *Eisena*, *Helodrilus* spp.)

Metastrongylus pudendotectus

Synonym: *Metastrongylus brevivaginatus*

Description: Differs from *M. apri* in having a larger bursa and smaller spicules (<1.5 mm long) with double hooks in the male. Males are about 16–18 mm and females 20–37 mm in length. The female possesses a straight tail. Eggs measure about 57–63 by 39–42 µm.

Life cycle: The prepatent period is about four weeks.

Metastrongylus salmi

Description: Similar to *M. pudendotectus* but with longer spicules, which are approximately 2 mm in length.

FAMILY PROTOSTRONGYLIDAE

See **life cycle 6**.

Muellerius

These are grey-reddish, slender hair-like worms about 1–4 cm long, which, although large, are often difficult to discern with the naked eye as they are embedded in lung tissue.

Life cycle: The life cycle is indirect and involves a molluscan intermediate host. The worms are ovoviviparous, the L_1 being passed in the faeces; these penetrate the foot of the molluscan intermediate host and develop to L_3 in a minimum period of 2–3 weeks. The sheep or goat is infected by ingesting the mollusc. The L_3, freed by digestion, travel to the lungs by the lymphatic–vascular route, the parasitic moults occurring in the mesenteric lymph nodes and lungs. The prepatent period of *Muellerius* is 6–10 weeks. The period of patency is very long, exceeding two years. The main species is *Muellerius capillaris* which infects the lung of sheep, goats, deer and wild ruminants. This parasite has slugs (*Limax*, *Agrolima* spp.) and snails (*Helix*, *Succinea* spp.) as intermediate hosts.

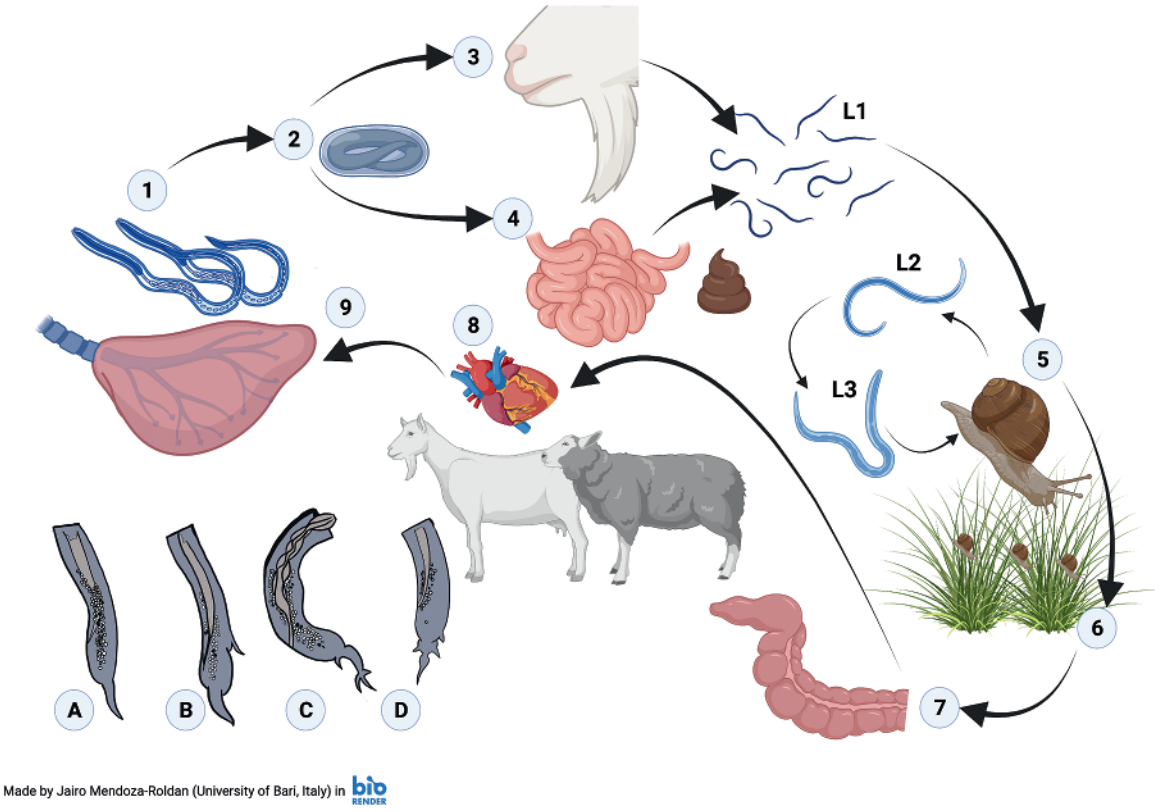
Muellerius capillaris

Description: Males are 12–24 mm and females 19–25 mm long. The posterior end of adult male *Muellerius* is spirally coiled and the bursa is very small and folded inwards. The spicules consist of a proximal alate region and two distal serrated arms. Two sclerotised rods represent the gubernaculum. Eggs measure about 100 by 20 µm and are unsegmented when laid and develop in the lungs before being passed as L_1 larvae in the faeces. The first-stage larva

LIFE CYCLE 6. LIFE CYCLE OF BRONCHOPULMONARY PROTOSTRONGILIDAE IN SHEEP AND GOATS

The four most common species of bronchopulmonary protostrongylids, also known as small bronchopulmonary strongylids of small ruminants, can be differentiated based on size, location in the lung of the host and morphology of the caudal end of the first-stage larvae (L_1) (A – *Protostrongylus rufescens*, B – *Muellerius capillaris*, C – *Cystocaulus ocreatus*, D – *Neostrongylus linearis*).

In definitive hosts, adult protostrongylids live in the lungs (1). After mating, the females release eggs (2) that hatch into L_1; these are excreted in the external environment through the expectorate and nasal mucus (3) and, more frequently, via the faeces (4) after having been swallowed enveloped in bronchial catarrh. In order to become infective, the larvae require passage through pulmonate gastropods, that act as intermediate hosts (5); larvae penetrate the foot of these hosts and moult from L_1 to L_2 and L_3. Small ruminants acquire the infection by ingesting infected intermediate hosts (6). Once ingested, the L_3 penetrate the intestinal submucosa (7) and, via the circulatory system, travel to the mesenteric lymph nodes where they moult to fourth-stage larvae (L_4). The latter travel to the lung capillaries via the thoracic duct, vena cava and right heart (8). Once in the capillaries, the larvae penetrate the lung parenchyma and develop into adult worms in the secondary branches of the bronchi, in the alveoli or underneath the pleura (9), depending on species.



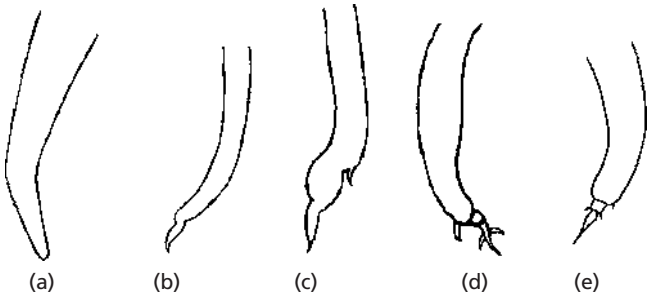


Fig. 1.59 Comparison of the posterior region of the first-stage larvae of (a) *Dictyocaulus filaria*, (b) *Protostrongylus rufescens*, (c) *Muellerius capillaris*, (d) *Cystocaulus ocreatus* and (e) *Neostrongylus linearis*.

has an S-shaped wavy tail (see Fig. 4.13c) and a small dorsal spine adjacent to the tip (Fig. 1.59c). It measures 300–320 µm and contains fine granules.

Protostrongylus

Adult worms are slender, hair-like, reddish worms found in the small bronchioles of the lung (Table 1.24).

Life cycle: The worms are ovoviviparous, the L_1 being passed in the faeces; these penetrate the foot of the molluscan intermediate host and develop to L_3 in a minimum period of 2–3 weeks. The final host is infected by ingesting the mollusc. The L_3, freed by digestion,

Table 1.24 *Protostrongylus* species.

Species	Hosts	Site	Intermediate hosts
Protostrongylus rufescens	Sheep, goats, deer, wild ruminants	Lung	Snails (*Helicella*, *Theba*, *Abida*, *Zebrina* spp.)
Protostrongylus brevispiculum	Sheep	Lung	Snails
Protostrongylus stilesi	Sheep	Lung	Snails
Protostrongylus skrjabini	Sheep	Lung	Snails
Protostrongylus rushi	Sheep	Lung	Snails
Protostrongylus davtiani	Sheep	Lung	Snails

travel to the lungs by the lymphatic–vascular route, the parasitic moults occurring in the mesenteric lymph nodes and lungs. The prepatent period of *Protostrongylus* is 5–6 weeks. The period of patency is very long, exceeding two years.

Protostrongylus rufescens

Description: Adult worms are slender and reddish; males measure up to 4.5 cm and females up to 6.5 cm. In the male, the bursa is well developed but small. The dorsal ray is globular in shape with six papillae on the ventral side. The spicules are almost straight; the distal ends bear two membraneous alae. The male worms can be differentiated from *D. filaria* by these long comb-like spicules. The gubernaculum has two boot-shaped prolongations bearing several knobs posteriorly. In the female, the vulva is close to the anus and the conoid tail. Both horns of the uterus extend anteriorly (prodelphic). This differs from *D. filaria* where the vulva is situated near the middle of the body and where the two horns of the uterus extend in opposite directions (amphidelphic). The eggs measure around 75–120 by 45–82 µm and are unsegmented when laid. The first-stage larva has a wavy outline with a pointed tail but is devoid of a dorsal spine (Fig. 1.59b). It measures 320–400 µm and contains fine granules.

Protostrongylus brevispiculum

Description: The adult worms are small and hair-like. In the male, the dorsal ray is small and rounded and the externodorsal rays are elongate. The spicules are much shorter than in *P. rufescens* and the gubernaculum consists of two parts that are smooth and pointed and curve medially and ventrally. The telamon is well developed.

Cystocaulus

Adult worms are slender, thread-like, dark-brown worms found in the small bronchioles of the lung.

Life cycle: Similar to *Muellerius*. The prepatent period is 5–6 weeks.

Cystocaulus ocreatus

Description: Male worms are up to 4–5 cm and females up to 9 cm long. In the male, the bursa is small; the spicules consist of a proximal cylindrical region joined distinctly to a distal lance-shaped region. The gubernaculum has a complex structure, with the posterior part consisting of two pointed boot-shaped structures. In the female, the vulva is protected by a bell-shaped expansion of the cuticle. The first-stage larva has a kinked tail and dorsal and ventral spine (Fig. 1.59d).

Spiculocaulus

The main species is *Spiculocaulus austriacus* which infects the lung of sheep and goats. This parasite has snails as intermediate hosts.

Neostrongylus

Small worms found in the lungs.

Life cycle: Similar to the other metastrongylid lungworms. The prepatent period in sheep is around 8–10 weeks. The main species is *Neostrongylus linearis* which infects the lung of sheep and goats. This parasite has snails as intermediate hosts.

Neostrongylus linearis

Description: Adult worms are small; the males are 5–8 mm and females 13–15 mm long. In the male, the spicules are unequal in size. The first-stage larva has a straight tail with a small dorsal and two small lateral spines (Fig. 1.59e).

Varestrongylus

Thread-like worms found in the lung parenchyma and bronchioles of sheep and goats (i.e. *Varestrongylus schulzi*), and of red deer and fallow deer (i.e. *V. sagittatus*, *V. capreoli*).

Life cycle: Ingested third-stage larvae present within the intermediate host migrate through the intestinal wall to the lymph nodes, migrating via the lymph and blood to the lungs. They then form 'breeding clusters' in which they grow to sexual maturity. Female worms are ovoviviparous with first-stage larvae coughed up and swallowed. When ingested by a molluscan intermediate host, the larvae develop to infective L_3 in 3–4 weeks.

Elaphostrongylus

The main species is *Elaphastrongylus cervi* (syn. *Elaphostrongylus rangiferi*) which infects the connective tissue and CNS of deer (red, roe, sika, reindeer). This parasite has slugs and snails as intermediate hosts.

Elaphostrongylus cervi

Synonym: *Elaphostrongylus rangiferi*

Description: The mature worms are long and slender. Males are up to 40 mm and females up to 60 mm long. First-stage larvae have a dorsal spine on the tail and measure 395–440 µm in length.

Life cycle: Female worms lay eggs that either hatch *in situ* or are carried to the lungs via the bloodstream and then hatch.

Larvae migrate through the lungs to the airways and are then swallowed and pass out in the faeces. The larvae may survive in the environment for up to two years before infecting a molluscan intermediate host. The parasites develop through the second-stage to the infective third-stage larvae in the mollusc within 27–50 days and can retain their infectivity for up to another two years. Deer become infected when they ingest snails containing infective larvae. After ingestion, the larvae burrow through the gut wall and migrate to the final tissue site, at the same time developing into adult worms. The prepatent period is about 112 days.

Parelaphostrongylus

The main species is *Parelaphostrongylus tenuis* (syn. *Odocoileostrongylus tenuis*, *Elaphostrongylus tenuis*) which infects the cranial meninges and CNS of white-tailed deer, moose, wapiti and others. This parasite has slugs and snails as intermediate hosts.

Parelaphostrongylus tenuis

Synonyms: *Odocoileostrongylus tenuis*, *Elaphostrongylus tenuis*

Description: The mature worms are long and thread-like; males are up to 40 mm and females up to about 90 mm long. First-stage larvae have a dorsal spine on the tail and measure about 350 µm.

Life cycle: Unembryonated eggs are released into the bloodstream and travel to the lungs where they lodge in the capillaries and complete their development to L_1 before moving to the alveoli, from where they are coughed up and swallowed and passed in the faeces. To develop further, they must penetrate or be eaten by a slug or snail. In the foot of the snail, the larvae develop through the second-stage to the infective third-stage larvae. Deer become infected when they accidentally ingest slugs or snails containing infective larvae. After ingestion, the larvae burrow through the gut wall and migrate to the CNS via the spinal nerves and spinal cord, at the same time developing into adult worms. The prepatent period is about 82–137 days.

FAMILY FILAROIDIDAE

Oslerus

This genus was part of the larger genus *Filaroides*, but has now been separated on morphological grounds from the other members. Though distinction has been made on morphology, it is also useful from the veterinary standpoint, for it separates the single harmful species, *Oslerus osleri*, living in the upper air passages, from the relatively harmless species which are retained in the genus *Filaroides* and which live in the lung parenchyma. *Oslerus*, and its closely related genus *Filaroides*, are exceptional in the superfamily Metastrongyloidea in having direct life cycles.

Life cycle: The females are ovoviviparous and most eggs hatch in the trachea. Many larvae are coughed up and swallowed and passed in the faeces and infection may occur by ingestion of these; more commonly, transmission occurs when an infected bitch licks the pup and transfers the newly hatched L_1, which are present in her sputum. After ingestion, the first moult occurs in the small intestine and the L_2 travel to the lungs by the lymphatic–vascular route. Development through to L_5 takes place in the alveoli and bronchi, and the adults migrate to their predilection site, the tracheal bifurcation. The prepatent period varies from 10 to 18 weeks.

Oslerus osleri

Description: The worms, which are embedded in fibrous nodules in the trachea in the region of the bifurcation and in the adjacent bronchi, are small, pale and slender; males are 5 mm and females 9–15 mm long and slightly thicker. The tail of the male is rounded without obvious bursal lobes and bears a few papillae. The short spicules are slightly unequal. In the female the vulva is located close to the anus. The larva has a short S-shaped tail and measures 232–266 µm in length. The medium-sized eggs have thin shells, measure around 80 by 50 µm and contain a larva.

Oslerus rostratus

Synonyms: *Anafilaroides rostratus*, *Filaroides rostratus*

Description: The adult males are about 28–37 mm long and the adult females 48–64 mm long. The vulva in the female is located just anterior to the anus.

Filaroides

The worms (Table 1.25) are very small (0.5–1 cm long), slender, hair-like and greyish, and are not only difficult to see with the naked eye in the lung parenchyma but are also unlikely to be recovered intact from the tissue. These lungworms have a direct life cycle.

Filaroides hirthi

Description: The worms are very small (0.5–1 cm long), slender, hair-like and greyish, and are not only difficult to see with the naked eye in the lung parenchyma but are unlikely to be recovered intact from the tissue. *Filaroides hirthi* is smaller than *F. milksi* (see next section). The L_1, present in the faeces and sputum, are coiled and the tail has a notch, followed by a constriction, and has a terminal lance-like point. Larvae measure about 240–290 µm.

Life cycle: The life cycle is direct. The worms are ovoviviparous and the hatched L_1 are passed in faeces or expelled in sputum. Though infection may be acquired by ingestion of faecal larvae, the important route, as in *Oslerus* infection, is thought to be by transfer of L_1 in the bitch's saliva when the pup is licked. The prepatent period of *F. hirthi* is around five weeks.

Table 1.25 *Filaroides* species.

Species	Hosts	Site
Filaroides hirthi	Dogs	Lung
Filaroides milksi (syn. *Andersonstrongylus milksi*)	Dogs	Lung
Filaroides bronchialis (syn. *Filaroides martis*)	Mink, polecats, other Mustelidae	Lung

Filaroides milksi

Description: As for *F. hirthi*. *Filaroides milksi* is larger than *F. hirthi*.

FAMILY ANGIOSTRONGYLIDAE

Angiostrongylus

Three main species are reported within this genus (Table 1.26).

Angiostrongylus vasorum

Description: These are small reddish worms. The slender males measure 14–18 mm and the stouter females 18–25 mm in length. Males have a small bursa and females have a 'barber's pole' appearance with the white ovaries coiled round the red intestine, similar to that in *Haemonchus*. The ventral rays are fused for most of their length and the dorsal ray is stout with stout terminal branches. In the female, the white ovaries are coiled round the red intestine (Fig. 1.60) with the vulva in the posterior half of the body. Eggs are unsegmented when laid in the lung and measure about 70–80 by 40–50 µm. First-stage larvae are 330–360 µm in length and have a small cephalic button and a wavy tail with a subterminal notch (see Fig. 4.13e).

Life cycle: The genus is ovoviviparous. The adult worms in the larger pulmonary vessels lay eggs, which are carried to the capillaries, where they hatch. The L_1 break into the alveoli, migrate to the trachea and thence to the alimentary tract to be passed in the faeces. Further development takes place after entry into the intermediate host, the infective third stage being reached in 17 days. After the mollusc has been ingested by the dog, the infective L_3, freed by digestion, travel to the lymph nodes adjacent to the alimentary tract, where both parasitic moults take place, and then to the vascular predilection site. L_5 have also been found in the liver. The prepatent period is around seven weeks, and the worms can live in the dog for more than two years.

Table 1.26 *Angiostrongylus* species.

Species	Hosts	Site	Intermediate hosts
Angiostrongylus vasorum	Dogs, foxes	Heart, pulmonary vessels	Slugs and snails
Angiostrongylus cantonensis	Rats, humans	Pulmonary artery (rats), meninges (humans)	Slugs and snails
Angiostrongylus costaricensis	Rats, humans	Ileocaecal arteries (rats), intestines (humans)	Slugs and snails

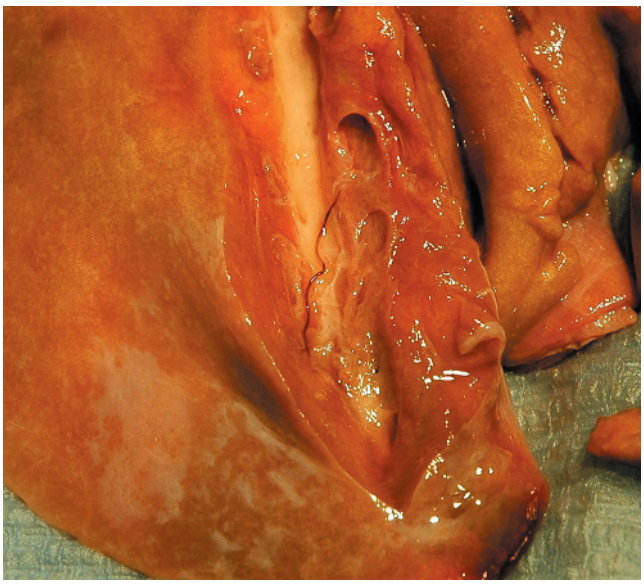


Fig. 1.60 Female *Angiostrongylus vasorum* in the pulmonary artery.

Angiostrongylus cantonensis

Description: The body is filariform and tapered at both ends. Males measure about 18 mm and females 23 mm in length. Fresh female worms have a 'barber's pole' appearance as the white uterine tubules spiral round the blood-filled intestine. The slender spicules are of equal length and are striated. A gubernaculum is present. The ovoid eggs laid in the pulmonary arteries are thin-shelled, transparent and unembryonated.

Life cycle: Infection is acquired through ingestion of a mollusc containing L_3 larvae. The larvae are released in the digestive tract and migrate via the hepatic portal system and lungs to the central nervous system where they undergo two moults. The young worms eventually migrate via the cerebral vein to the pulmonary arteries. The adult worms mate and lay eggs that pass to the capillaries; these eggs embryonate and hatch and L_1 larvae enter the alveoli and eventually are coughed up, swallowed and pass out in the faeces. These larvae are about 270–300 µm long. The L_1 are ingested by, or penetrate, the intermediate host. The prepatent period is around six weeks.

Angiostrongylus costaricensis

Description: The worms are tapered at both ends and are filiform in shape. Males measure about 20 mm and females 30–40 mm in length. The spicules are equal in length, slender and striated. The cephalic ends of the spicules are blunt and the caudal tips are pointed. A gubernaculum is present. The ovoid eggs laid in the mesenteric arterioles are thin-shelled, transparent and unembryonated. The embryonated eggs shed in faeces measure around 90 µm.

Life cycle: Larvae are shed in the faeces of the rodent and are ingested by a mollusc in which development to the L_3 stage takes place. Following ingestion of the mollusc by rats, or ingestion of vegetation contaminated with infective mucous trails, the L_3 migrate via the lymphatics. After two moults, the worms migrate to the ileocaecal arteries where they mature, reproduce and lay eggs, which are then carried to the intestinal wall. Eggs embryonate

and hatch to L_1 larvae which migrate to the lumen of the intestine and pass out in the faeces. The prepatent period is around 3–4 weeks.

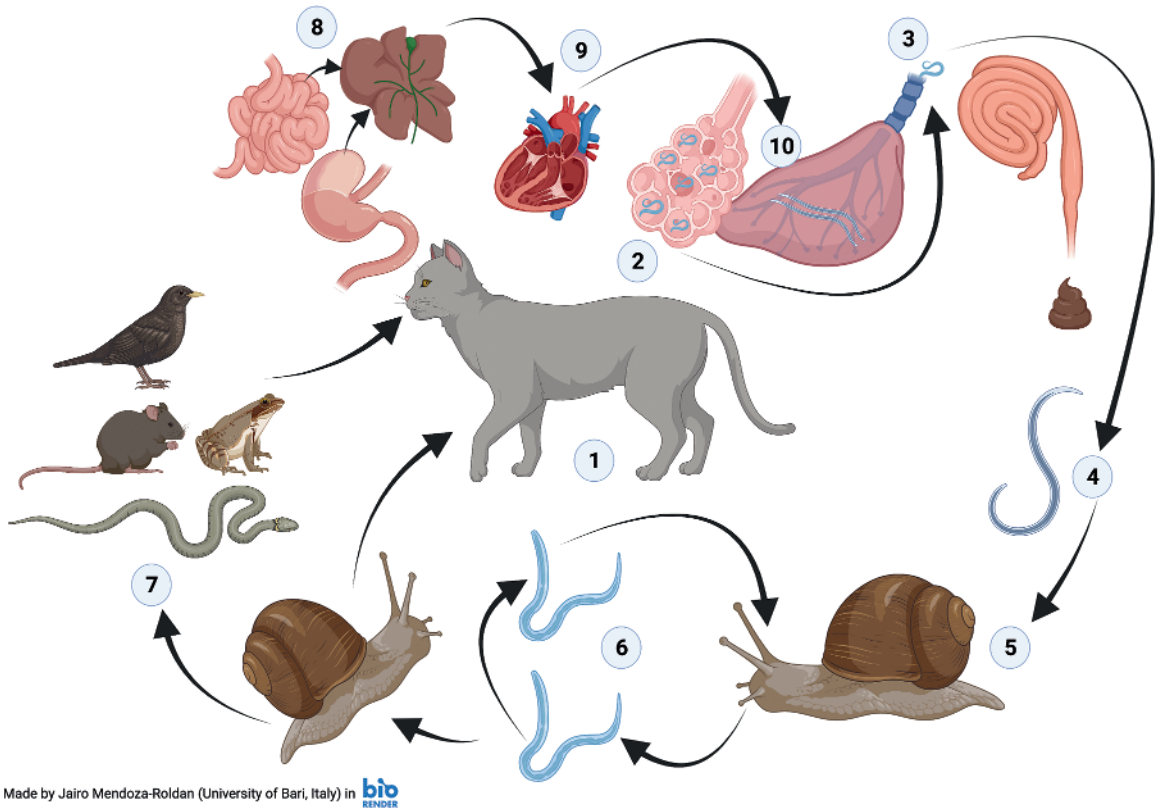
Aelurostrongylus

The genus consists of one species, *Aelurostrongylus abstrusus*, which is common in the lungs of the domestic cat.

Life cycle: The life cycle is indirect. The worms are ovoviviparous, and the L_1 are passed in the faeces. These penetrate the foot of the molluscan intermediate host and develop to the infective L_3 and during this phase paratenic hosts, such as birds and rodents, may eat the mollusc. The cat is usually infected by ingestion of these paratenic hosts and less frequently by ingestion of the intermediate hosts. The L_3 released in the alimentary tract travel to the lungs by the lymphatics or bloodstream. After the final moult, the adults are located in the alveolar ducts and the terminal bronchioles. The prepatent period is between four and six weeks, and the duration of patency is about four months, though some worms may survive in the lungs for several years despite the absence of larvae in the faeces. This parasite has slugs and snails as intermediate hosts. See **life cycle 7**.

LIFE CYCLE 7. LIFE CYCLE OF *AELUROSTRONGYLUS ABSTRUSUS*

Adults of *Aelurostrongylus abstrusus* live in the bronchioles and alveolar ducts of cats (1), that act as definitive hosts. After mating, the females release elliptical eggs (2) containing larvae (L_1) that, after hatching, travel up the respiratory system and are either eliminated with the expectorate or, more frequently, swallowed and excreted with the faeces (3). In the external environment (4), the larvae penetrate terrestrial molluscs that act as intermediate hosts (5); inside these hosts, the larvae moult twice to reach the infective, third-larval stage (6). The intermediate hosts may be ingested by parastenic hosts, e.g. reptiles, amphibians, rodents and birds (7). Cats acquire the infection by ingesting infected intermediate or paratenic hosts. Following infection, the larvae migrate via the circulatory system through several organs (8, 9) before reaching the respiratory tract (10), where they develop into sexually mature adult nematodes within four weeks.



Aelurostrongylus abstrusus

Description: Aggregations of worms, eggs and larvae are present throughout the lung tissue. The worms, about 1 cm long, are very slender and delicate, and are difficult to recover intact for examination; a squeeze preparation from a cut surface of the lung will show the worm material including the characteristic L_1, which bear a subterminal spine on their S-shaped tail (Fig. 1.61). The male bursa is short and the lobes are indistinct. The spicules are stout. Eggs have a thin shell, measure around 70–80 by 50–75 µm and embryonate in the lung. L_1 in faeces are short and thick with a conical anterior they are about 360–400 µm long with granular contents.

FAMILY CRENOSOMATIDAE

This family includes several species that infect trachea, bronchi, bronchioles of many animal species. In particular, *Crenosoma vulpis* infects dogs, foxes and wolves, and *Troglostrongylus brevior* domestic and wild felids.

Life cycle: Adult females deposit thin-shelled eggs containing first-stage larvae (L_1), which ascend the trachea and pass into the intestinal tract and out in the faeces. These larvae penetrate the foot of the intermediate molluscan host and are present as infective third-stage larvae (L_3) in about three weeks. After ingestion of the molluscan host by the final host, the L_3 are released by digestion and travel to the lungs, via the lymphatic glands and hepatic circulation, where both parasitic moults take place. The prepatent period is around three weeks. The transmammary transmission of *Troglostrongylus brevior* has been demonstrated being this parasite infection of major concern in kittens.

Crenosoma vulpis

Description: Slender white worms, up to 1.5 cm long. Males are 4–8 mm with well-developed bursae with a large dorsal ray. Females are 12–16 mm. The two horns of the uterus extend in opposite directions (amphidelphic). The ovejector sphincter is prominent. The host and site are usually sufficient for generic diagnosis. Microscopic confirmation is based on the presence of annular crenated folds of the cuticle, which bear small backwardly directed spines on their margins. Larvae are about 265–330 µm in length and have a straight pointed tail.

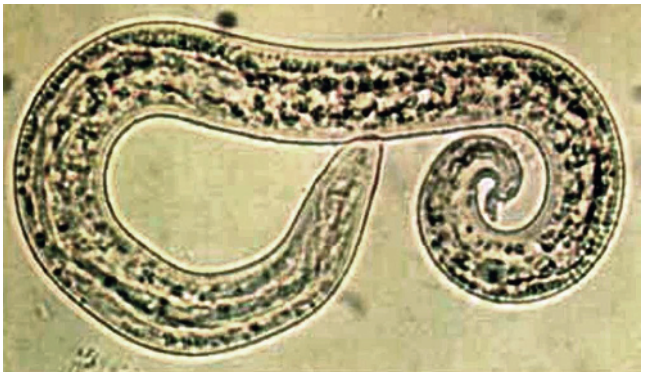


Fig. 1.61 *Aelurostrongylus abstrusus* L_1: S-shaped tail bears a subterminal spine.

Troglostrongylus brevior

Description: Adults are slender worms located in the frontal sinuses and bronchi of the definitive hosts. The female worms are up 1.3 cm long (longer than *A. abstrusus*) with a cuticle finely striated with transverse striations and inflated at the apical and caudal ends where it throws into folds. In the male, the bursa is small in comparison with the total body size and is supported by short rays. The dorsal ray of *T. brevior* is elongated with two pairs of papillae and externodorsal and anterolaterals rays arising independently while postero- and mediolaterals are partially fused. Spicules of *T. brevior* are 510–631 µm long, each terminating with a thin and long appendage and four small digitiform projections.

Considering the strong similarities between the first-stage larvae (L_1) and those of the better known *Aelurostrongylus abstrusus*, their identification is often challenging and the actual impact of these lungworm infestations has yet to be fully appreciated. First-stage larvae of *T. brevior* are 300–357 µm long and present a pointed anterior extremity and a subterminal (dorsal) oral opening (in *A. abstrusus* the oral opening is terminal).

SUPERFAMILY RHABDITOIDEA

This is a primitive group of nematodes which are mostly free-living, or parasitic in lower vertebrates and invertebrates. *Rhabdias* are respiratory parasites in reptiles. A few normally free-living genera such as *Halicephalobus* (*Micronema*) and *Rhabditis* occasionally cause problems in animals.

FAMILY PANAGROLAIMIDAE

Halicephalobus (syn. *Micronema*)

Occasional cases of infection of horses with the saprophytic free-living nematode *Halicephalobus deletrix* (syn. *Halicephalobus gingivalis*, *Micronema deletrix*) have been described from various parts of the world. In affected animals the very small worms, less than 0.5 mm in length, have been found in nasal and maxillary granulomas and in the brain and kidney.

FAMILY RHABDITIDAE

Rhabditis

Several members of this free-living genus of nematodes may become casual parasites, the larvae invading the skin and causing an intense pruritus. The larvae do not migrate but die and so adults are not present in animals. Cases have been most frequently reported in dogs housed in kennels with damp hay or straw bedding and the lesions, usually confined to areas of the body in contact with the ground, show hair loss, erythema and pustule formation if infected with bacteria. The very small worms (1–2.8 mm in length)

with a rhabditiform oesophagus may be recovered from skin scrapings. Treatment is symptomatic and the condition can be prevented by housing animals on clean dry bedding. *Rhabditis* infection has also been associated with otitis externa in cattle in the tropics. The main species is *Rhabditis strongyloides* (syn. *Pelodera strongyloides*) which infects the subcutaneous tissue and skin of dogs, cattle and horses.

FAMILY RHABDIASIDAE

Lungworms of the genus *Rhabdias* are common parasites of amphibians and reptiles, with about 60 species reported worldwide.

Life cycle: Only females are parasitic and these produce larvated, oval, thin-shelled eggs. After hatching, larvae may develop through four larval stages into free-living adult male and female worms and this can be followed by a succession of free-living generations. Infection is usually via the oral route (but percutaneous infection is also possible) and larvae penetrate the oesophageal tissue and then pass via the body cavity and primarily reside near the lower lung as ungravid adults. These adults then penetrate the lungs and feed on blood, becoming gravid and passing embryonated eggs in the faeces. Usually no intermediate hosts are involved. However, transport hosts such as physid snails, earthworms or frogs can be involved for some *Rhabdias* species.

SUPERFAMILY STRONGYLOIDIDEA

FAMILY STRONGYLOIDIDAE

Strongyloides

Members of this genus are common parasites of the small intestine in very young animals and although generally of little pathogenic significance, under certain circumstances may give rise to severe enteritis.

These worms (Table 1.27) are slender, hair-like, colourless worms generally less than 10 mm long and only the female worms are parasitic. The long cylindrical oesophagus (typically rhabditiform in shape) may occupy up to one-third of the body length and the filamentous uterus is intertwined with the intestine, giving the appearance of contorted twisted thread (Fig. 1.62). Unlike other intestinal parasites of similar size, the tail has a blunt point. Species identification is generally based on identification of the characteristic female worms, or eggs, in the host species.

Life cycle: *Strongyloides* is unique among the nematodes of veterinary importance, being capable of both parasitic and free-living reproductive cycles. The parasitic phase is composed entirely of female worms in the small intestine and these produce larvated eggs by parthenogenesis, i.e. development from an unfertilised egg. In herbivores, it is the larvated egg which is passed out in the faeces, but in other animals it is the hatched L_1. After hatching, larvae may develop through four larval stages into free-living adult male and female worms and this can be followed by a succession of free-living generations. However, under certain conditions, possibly related to temperature and moisture, the L_3 can become parasitic, infecting the host by skin penetration or ingestion and migrating via the venous system, the lungs and trachea to develop into adult female worms in the small intestine. Young animals may acquire infection immediately after birth from the mobilisation of arrested larvae in the tissues of the ventral abdominal wall of the dam, which are subsequently excreted in the milk. In addition, prenatal infection has been demonstrated experimentally in cattle. The prepatent period in most species is 8–14 days.

Table 1.27 *Strongyloides* species.

Species	Hosts	Site
Strongyloides papillosus	Sheep, cattle, goats, wild ruminants, rabbits	Small intestine
Strongyloides westeri	Horses, donkeys, zebras, rarely pigs	Small intestine
Strongyloides ransomi	Pigs	Small intestine
Strongyloides avium	Chickens, turkeys, geese, wild birds	Small intestine, caecae
Strongyloides stercoralis (syn. *Strongyloides canis*, *Strongyloides intestinalis*, *Anguillula stercoralis*)	Dogs, foxes, cats, humans, Old World monkeys, apes	Small intestine
Strongyloides planiceps	Cats	Small intestine
Strongyloides felis (syn. *Strongyloides cati*)	Cats	Small intestine
Strongyloides tumefaciens	Cats	Large intestine
Strongyloides ratti	Rats	Small intestine
Strongyloides cebus	New World monkeys	Small intestine
Strongyloides fulleborni	Old World monkeys, apes	Small intestine

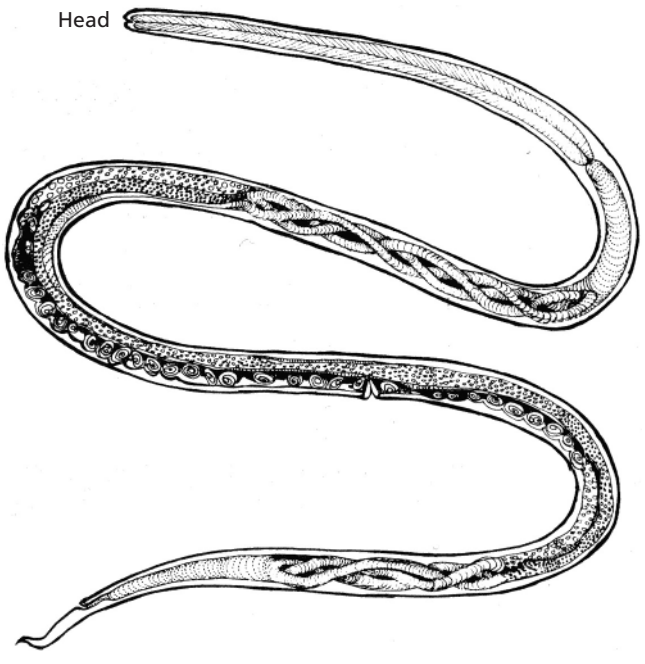
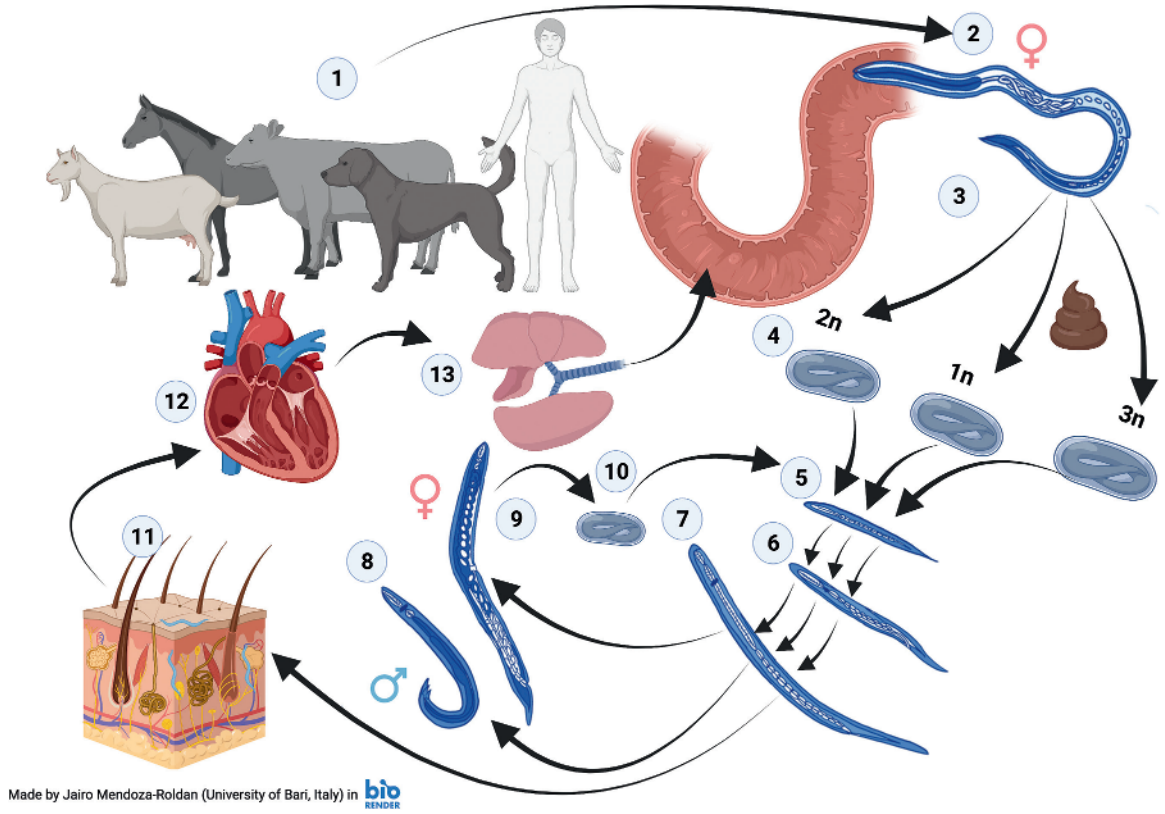


Fig. 1.62 *Strongyloides* spp. adult female.

LIFE CYCLE 8. LIFE CYCLE OF *STRONGYLOIDES* SPP.

Strongyloides infects several animal species (e.g. ruminants, equids, carnivores, pigs, birds), including humans (1). Adult females are the only parasitic life cycle stage; these are <1 cm long and characterised by a well-developed oesophagus (spanning one-third of the whole-body length) and uterus coiled around the intestine (2). Adult females live in the small intestine, where they reproduce by parthenogenesis, releasing larvated eggs (3). The eggs (35 × 45 µm) are oval in shape and with a thin outer membrane (4). They are excreted in the faeces of herbivore hosts while, in other hosts, they hatch in the intestine, thus releasing the L_1. The eggs are characterised by different chromosome numbers (n). Eggs 1n and 2n hatch L_1 (5) that, following moults to L_2 (6) and L_3 (7), develop into free-living males (8) and heterogametic females (9), respectively. The 3n type egg develops directly via L_1–L_3 into the homogonic female; this may occur via free L_3 on soil or inside the host's intestine (internal autoinfection cycle). Mating results in eggs (10) that may give rise to new free-living generations (8, 9) or develop via L_3 into parthenogenic females upon penetration into the vertebrate host (11). L_3, hatched from 3n eggs, penetrate the skin of the host (11) and, through the haemolymphatic circulation (12), travel to the lungs (13), where they may cause microhaemorrhages. After travelling up the trachea, larvae are swallowed and reach the intestine, where they develop into adult females that release larvated eggs by parthenogenesis.



Strongyloides papillosus

Description: Adult female worms are 3.5–6 mm long with an oesophagus 0.6–0.8 mm in length. *Strongyloides* eggs are oval with blunt poles and slightly barrel-shaped side walls, thin-shelled and small, being half the size of typical strongyle eggs. These colourless eggs have a smooth shell and measure about 43–60 by 20–25 µm and contain an L_1 larva. Infective larvae measure about 600 µm.

Strongyloides westeri

Description: Adult female worms are up to 9 mm long with an oesophagus measuring 1.2–1.5 mm in length. The long oesophagus may occupy up to one-third of the body length and the uterus is intertwined with the intestine, giving the appearance of twisted thread. Unlike other intestinal parasites of similar size, the tail has a blunt point. *Strongyloides* eggs are oval, thin-shelled, smooth and small (40–52 × 32–40 µm), being half the size of typical strongyle eggs (see Fig. 4.5). The side walls are symmetrical and the poles are wide and the egg contains a short thick larva. The hatched L_1 is passed out in the faeces.

Strongyloides ransomi

Description: Slender hair-like worms 3.4–4.5 mm long (Fig. 1.62). Only females are parasitic. The long oesophagus may occupy up to one-third of the body length and the uterus is intertwined with the intestine, giving the appearance of twisted thread. Unlike other intestinal parasites of similar size, the tail has a blunt point.

Strongyloides eggs are oval, thin-shelled and small, 45–55 by 26–35 µm. They have a very fine wall and always contain a thick, short, first-stage larva (see Fig. 4.6).

Life cycle: The prepatent period is 6–9 days.

Strongyloides avium

Description: Adult female worms are approximately 2 mm long with an oesophagus 0.7 mm in length. The long oesophagus may occupy up to one-third of the body length and the uterus is intertwined with the intestine, giving the appearance of twisted thread (Fig. 1.62). Unlike other intestinal parasites of similar size, the tail has a blunt point. *Strongyloides* eggs are oval, thin-shelled and small, 52–56 by 36–40 µm, being half the size of typical strongyle eggs. The larvated egg is usually passed in the faeces.

Strongyloides stercoralis

Synonyms: *Strongyloides canis*, *Strongyloides intestinalis*, *Anguillula stercoralis*

Description: Slender hair-like worms around 2 mm long. Only females are parasitic. The long oesophagus may occupy up to one-third of the body length and the uterus is intertwined with the intestine, giving the appearance of twisted thread. Unlike other intestinal parasites of similar size, the tail has a blunt point. *Strongyloides* eggs are oval, thin-shelled and small, 50–58 by 30–34 µm. The hatched L_1 is passed out in the faeces.

Strongyloides planiceps

Description: Parasitic females are 2.4–3.3 mm long (mean 2.8 mm). The tail of the parasitic female narrows abruptly to a blunt tip, and the worms have ovaries with a spiral appearance.

Strongyloides felis

Synonym: *Strongyloides cati*

Description: Similar to *S. planiceps*. Parasitic females of *S. felis* have a long tail narrowing slowly to the tip. Ovaries are straight.

Strongyloides tumefaciens

Description: The parasitic females are 5 mm long and found in tumours of the large intestine.

SUPERFAMILY ASCARIDOIDEA

The ascaridoids are among the largest nematodes and occur in most domestic animals, both larval and adult stages being of veterinary importance. While the adults in the intestine may cause unthriftiness in young animals, and occasional obstruction, an important feature of the group is the pathological consequences of the migratory behaviour of the larval stages.

With a few exceptions, the genera have the following characteristics in common. They are large, white or cream, opaque worms that inhabit the small intestine. There is no buccal capsule, the mouth consisting simply of a small opening surrounded by three large conspicuous lips. A posterior bulb is usually absent from the oesophagus. The males possess two spicules but do not have a bursa. The common mode of infection is by ingestion of the thick-shelled egg containing the L_2. However, the cycle may involve transport and paratenic hosts.

Genera of veterinary interest include *Ascaris*, *Toxocara*, *Toxascaris*, *Parascaris*, *Ascaridia*, *Heterakis*, *Porrocaecum*, *Bayliascaris*, *Baraspidodera* and to a lesser extent the anisakids (Anisakidae: *Anisakis*, *Contracaecum*, *Hysterothylacium*, *Pseudoterranova*). Other acaridoids occur in reptiles and include *Ophidascaris* and *Polydelphus* found in snakes and *Angusticaecum* and *Sulcascaris* found in chelonia.

FAMILY ASCARIDIDAE

Ascaris

The genus includes large, stout, white worms, around 15–40 cm in length, infecting the small intestine of pigs (*Ascaris suum*) and humans (*Ascaris lumbricoides*).

Ascaris suum

Description: *Ascaris suum* is by far the largest nematode of the pig; the white/cream-coloured rigid females are up to 40 cm long and the males up to 25 cm in length (Fig. 1.63), and could only be confused with *Macracanthorhynchus* where this occurs. The dorsal lip possesses two double papillae, and each ventrolateral lip has one double papilla and a small lateral papilla. These lips have a row of very small denticles on their interior surface. The oesophagus is about 6.5 mm long and simple in shape. The male spicules are stout and the males tend to be slightly curved posteriorly. The eggs are ovoid and yellowish-brown, with a thick shell, the outer layer of which is irregularly mamillated (see Fig. 4.6). They measure 50–75 by 40–55 µm and the contents consist of granules and unsegmented cells. The egg is larvated when passed in the faeces and the thick multilayered eggshell enables the egg to survive desiccation and

Fig. 1.63 *Ascaris suum* adult worms.

freezing in the environment for several years. Occasionally, the population of worms will comprise only females and unfertilised eggs can appear in the faeces. Where an outer albuminous layer is present, it is thinner than that of a fertilised egg.

Life cycle: The life cycle is direct. Though the preparasitic moults occur by about three weeks after the egg is passed, a period of maturation is necessary and the egg is not usually infective until a minimum of four weeks after being passed, even in the optimal temperature range of 22–26°C. The egg is very resistant to temperature extremes, and is viable for more than four years. After ingestion, the larvated egg hatches in the small intestine, the L_3 larva penetrates the intestinal mucosa and then travels to the liver. The larva then passes in the bloodstream to the lungs and thence to the small intestine via the bronchi, trachea and pharynx. In the intestine, the final moult occurs and the young adult worms inhabit the lumen of the small intestine. If the eggs are ingested by an earthworm or dung beetle, they will hatch and the L_3 travel to the tissues of these paratenic hosts, where they can remain, fully infective for pigs, for a long period. The prepatent period is 7–9 weeks, and each female worm is capable of producing more than 200 000 eggs per day. Longevity is around 6–9 months.

Ascaris lumbricoides

Description: Male worms are 15–31 cm long and the posterior end is curved ventrally and has a bluntly pointed tail. Female worms are 20–49 cm long with the vulva located in the anterior end, which accounts for about one-third of its body length. The egg is ovoid and yellowish-brown, with a thick shell, the outer layer of which is irregularly mamillated (Fig. 1.64).

Toxocara

Nematodes in this genus (Table 1.28) are large white/cream-coloured worms, with females up to 18 cm and males up to 10 cm in length. There are no interlabia or intestinal caeca.

Toxocara canis

Description: Adult male worms measure up to 10 cm and females 18 cm in length, although the size can vary considerably (Fig. 1.65). The adult head is elliptical due to the presence of a pair of large

Table 1.28 *Toxocara* species.

Species	Hosts	Site
Toxocara canis	Dogs, foxes	Small intestine
Toxocara mystax (syn. *Toxocara cati*)	Cats	Small intestine
Toxocara malayiensis	Cats	Small intestine
Toxocara vitulorum (syn. *Neoascaris vitulorum*)	Buffalo, cattle	Small intestine

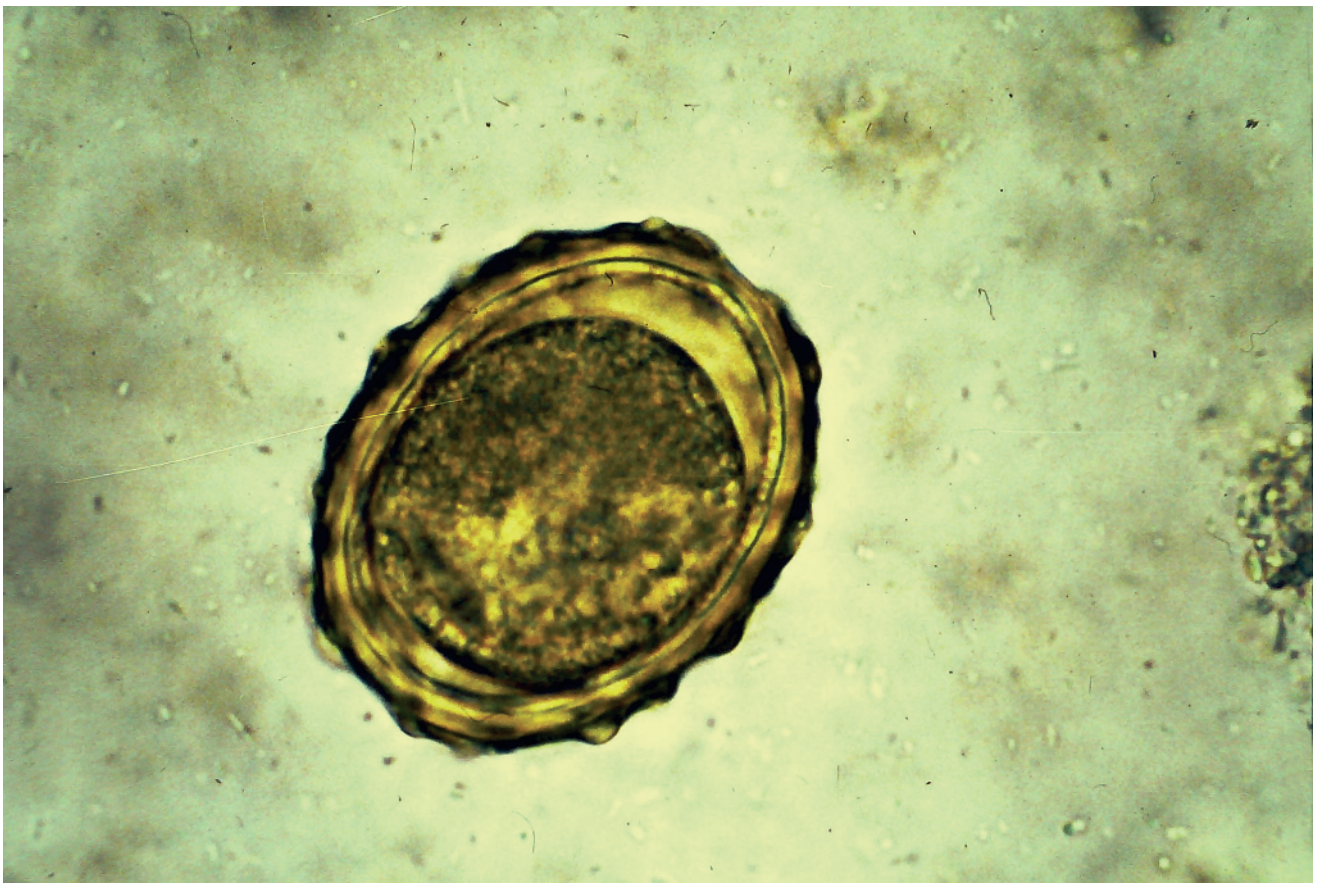


Fig. 1.64 *Ascaris* egg.

Fig. 1.65 Heavy *Toxocara canis* infection in the small intestine of a pup.

lanceolate cervical alae and the anterior body is curved ventrally. The mouth is surrounded by three large lips. There is no buccal capsule and the oesophagus lacks a posterior bulb. The tail of the male has caudal alae and a narrow terminal appendage. Female genital organs extend both anteriorly and posteriorly to the vulval area. The medium-sized egg is dark brown and subglobular, with a thick rough pitted shell. The granular unsegmented contents are very dark and normally fill the whole volume of the shell. Eggs measure 90 by 75 µm. The egg is very similar to that of *Parascaris*.

Life cycle: This species has the most complex life cycle in the superfamily, with four possible modes of infection. The basic form is typically ascaridoid, the egg containing the L_3 being infective, at optimal temperatures, four weeks after being passed. After ingestion, and hatching in the small intestine, the larvae travel by the bloodstream via the liver to the lungs, where the second moult occurs. The larvae then return via the trachea to the intestine where the final two moults take place. This form of ascaridoid migration occurs regularly only in dogs of up to about 2–3 months old.

In dogs over three months of age, hepatic–tracheal migration occurs less frequently and at around 4–6 months, it has almost ceased and is replaced by somatic migration, followed by hypobiosis. However, some dogs will support hepatic–tracheal migration as adults. Instead of hepatic–tracheal migration, the L_3 travel to a wide range of tissues including the liver, lungs, brain, heart and skeletal muscle, and the walls of the alimentary tract.

In the pregnant bitch, prenatal infection occurs, larvae becoming mobilised at about three weeks prior to parturition and migrating to the lungs of the fetus where they moult just before birth. In the newborn pup, the cycle is completed when the larvae travel to the intestine via the trachea, and the final moults occur. A bitch, once infected, will usually harbour sufficient larvae to infect all her subsequent litters, even if she never again encounters the infection. A few of these mobilised larvae, instead of going to the uterus, complete the normal migration in the bitch, and the resulting adult worms produce a transient but marked increase in faecal *Toxocara* egg output in the weeks following parturition.

The suckling pup may also be infected by ingestion of L_3 in the milk during the first three weeks of lactation. There is no migration in the pup following infection by this route. Paratenic intermediate hosts such as rodents, sheep, pigs or birds may ingest the infective eggs and the L_3 travel to their tissues where they remain until eaten by a dog, when subsequent development is apparently confined to the gastrointestinal tract.

A final complication is recent evidence that bitches may be reinfected during late pregnancy or lactation, leading directly to transmammary infection of the suckling pups and, once patency is established in the bitch, to contamination of the environment with eggs. The bitch may be reinfected via the ingestion of larval stages from the fresh faeces of puppies through her coprophagic activities. See **life cycle 9**.

The known minimum prepatent periods are as follows.

- Direct infection following ingestion of eggs or larvae in a paratenic host: 4–5 weeks.
- Prenatal infection: 2–3 weeks.

Toxocara mystax

Synonym: *Toxocara cati*

Description: Typical of the superfamily, *Toxocara mystax* is a large white/cream-coloured worm (up to 10 cm in length), often occurring as a mixed infection with the other ascarids of cats, such as *Toxascaris leonina*. Males are 3–6 cm and females 4–10 cm in length. The tail of the male has a terminal narrow appendage. Differentiation is readily made between *Toxocara mystax* and *Toxascaris leonina* on gross examination or with a hand lens, when the cervical alae of the former are seen to have an arrowhead form, with the posterior margins almost at a right angle to the body, whereas those of *Toxascaris* taper gradually into the body (Fig. 1.66a). The male, like that of *Toxocara canis*, has a small finger-like process at the tip of the tail. The egg is subglobular with

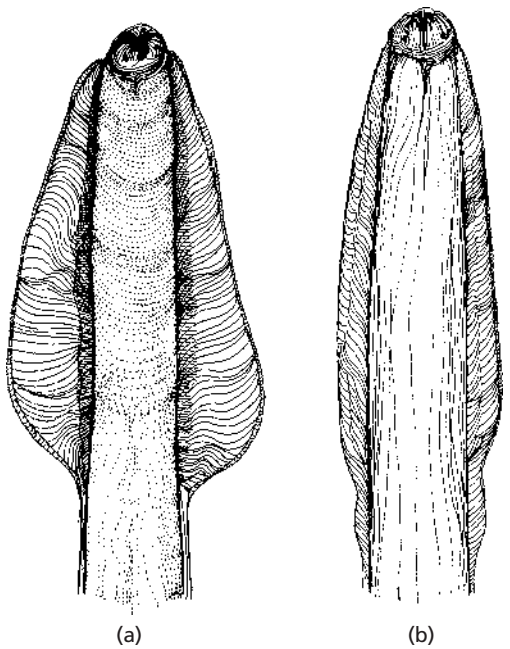
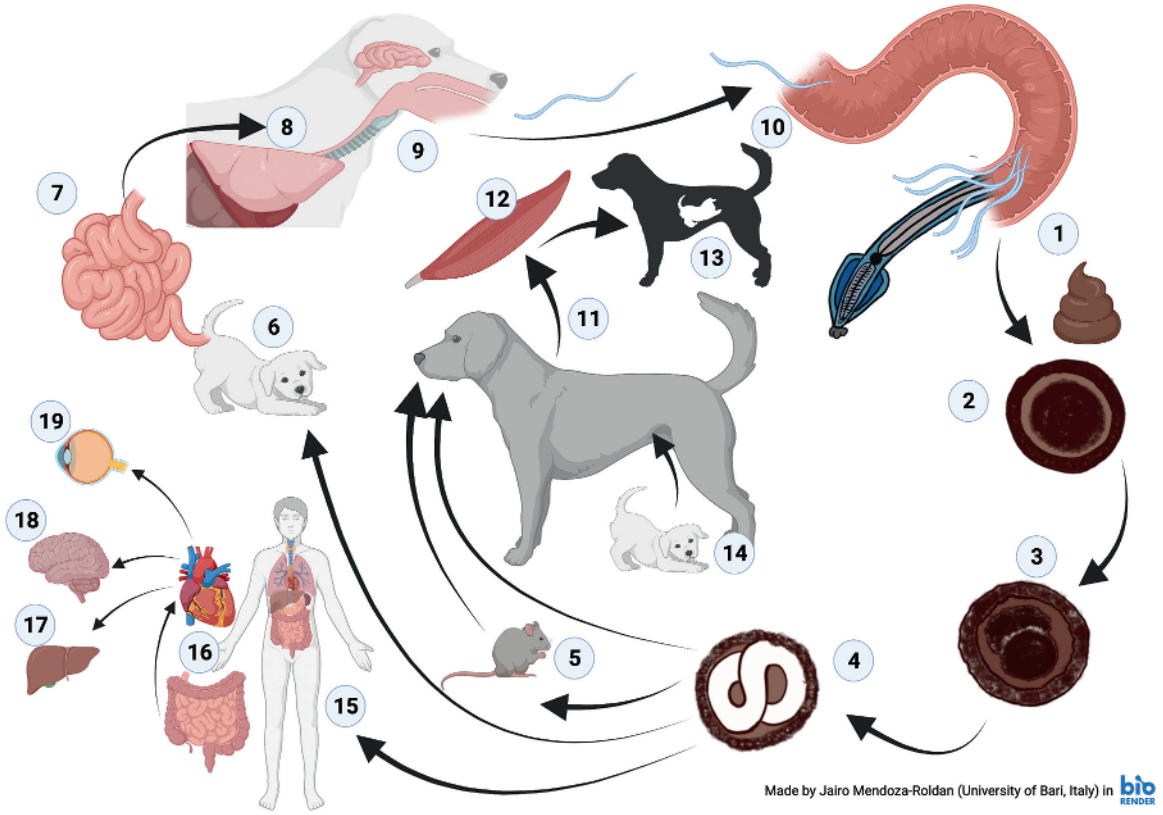


Fig. 1.66 Comparison of the anterior region of (a) *Toxocara mystax* and (b) *Toxascaris leonina*. The cervical alae of *Toxocara mystax* are arrow-shaped whereas those of *Toxascaris leonina* are more slender and less protrusive.

LIFE CYCLE 9. LIFE CYCLE OF *TOXOCARA CANIS*

Toxocara canis lives in the intestine of the dog (1), which acts as definitive host and sheds the nematode eggs with the faeces (2); these are spherical and characterised by a beehive-like outer shell encased in albuminous material. The egg contains a single undifferentiated embryo that, once in the external environment, matures (3) into an infective second-stage larva (4). The dog becomes infected by ingesting the larvated egg or paratenic hosts harbouring larvae in somatic tissues (5). Following ingestion of a larvated egg by a dog <3 months in age, an entero-hepatic-pneumo-tracheo-enteric migration occurs (6). In particular, the eggs hatch in the gastrointestinal tract (7) and, via the circulation, the larvae travel to the liver. Here, the larvae moult and, via the suprahepatic veins, reach the lungs (8), migrate up to the larynx and pharynx (9), and are swallowed to reach the intestine, where they mature to adult nematodes (10).

In dogs >3 months of age, this migration is gradually replaced by a visceral or somatic migration (11) whereby, following ingestion of larvated eggs, larvae migrate via the haemolymphatic circulation to several organs and tissues (e.g. liver, lung, heart, kidneys and skeletal muscles, 12) where they become latent. In male dogs, this phase marks the end of the life cycle; conversely, in pregnant bitches, the larvae become mobilised and migrate transplacentally to the livers of the fetuses (13). After birth, the larvae migrate to the lungs, moult, travel up the respiratory system and are swallowed, thus reaching the intestine where they develop into adult nematodes. Puppies can also acquire the infection via transmammary transmission (14), as mobilised larvae of *T. canis* are also excreted in the colostrum and milk. In humans (15), accidental ingestion of larvated eggs results in entero-pneumo-somatic migration of larvae (16), that cause visceral *larva migrans* (17), encephalic *larva migrans* (18) or ocular *larva migrans* (19), depending on where migration occurs.



a thick, rough, pitted shell. The granular unsegmented contents are dark brown to black in colour and usually occupy the whole volume of the shell. Eggs measure 65 by 75 µm and are characteristic in cat faeces.

Life cycle: The life cycle of *T. mystax* is migratory when infection occurs by ingestion of the L_2 in the egg, and non-migratory after transmammary infection with L_3 or after ingestion of a paratenic host. Following ingestion of eggs containing an infective second-stage larva, the larvae enter the stomach wall and then migrate via the liver, lungs and trachea back to the stomach and moult to L_3, while L_4 occur in the stomach contents, the intestinal wall and bowel contents. Rodent infections also play an important part in the life cycle. In these, larvae remain as second-stage forms but when an infected mouse is eaten by a cat, the larvae, liberated by digestion, enter the stomach wall of the cat and develop to L_3. As well as mice acting as 'intermediate hosts', L_2 may be found in the tissues of earthworms, cockroaches, chickens, sheep and other animals fed infective eggs. Transmammary infection is common throughout lactation, particularly in acutely infected cats, and the lactogenic route of transmission is the most important. Prenatal infection through the placenta does not occur, which is

dissimilar to *T. canis*. The prepatent period from egg infection is about eight weeks.

Toxocara malayiensis

Description: *Toxocara malayiensis* is a large white worm, typically 3 to 15 cm in length. It is morphologically similar to *T. canis* in dogs. There are three well-defined lips, each with a deep median notch lined with denticles: a dorsal lip with two large outer papillae, and two subventral lips each with one outer papilla. Cervical alae arise immediately behind the lips, gradually increasing in width to mid-length, then tapering gradually posteriorly.

Life cycle: The life cycle has not been fully described.

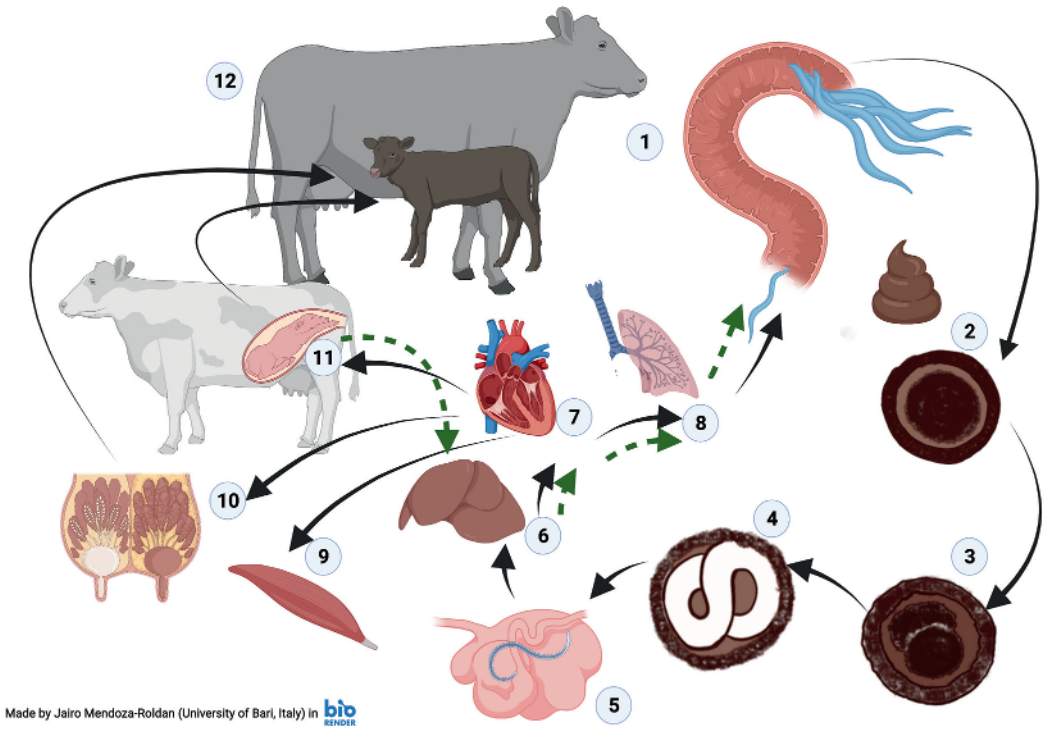
Toxocara vitulorum

Description: This is a very large whitish nematode. The adult male is up to 25 cm and the female up to 30 cm in length. The cuticle is less thick than other ascarids and somewhat soft and translucent. There are three lips, broad at the base and narrowing anteriorly. The oesophagus is 3–4.5 mm long and has a posterior granular ventriculus. The tail of the male usually forms a small spike-like appendage. There are about five pairs of postcloacal papillae; the anterior pair is large and double. Precloacal papillae are variable in number. The vulva is situated about one-eighth of the body length from the anterior end. The medium-sized egg of *T. vitulorum* is subglobular, with a thick, finely pitted albuminous shell, is almost colourless and measures 75–95 by 60–74 µm. The egg is unsegmented and the granular contents frequently only occupy part of the internal volume.

Life cycle: The most important source of infection is the milk of the dam, in which larvae are present for up to 3–4 weeks after parturition. There is no tissue migration in the calf following milk-borne infection and the prepatent period is 3–4 weeks. The ingestion of larvated eggs by calves over six months of age seldom results in patency, the larvae migrating to various tissues where they remain dormant; in female animals, resumption of development in late pregnancy allows further transmammary transmission. See **life cycle 10**.

LIFE CYCLE 10. LIFE CYCLE OF *TOXOCARA VITULORUM*

Adults of *Toxocara vitulorum* live in the small intestine of cattle (1) and excrete the parasite eggs via the faeces; the eggs are spherical and characterised by a granular outer shell (2). In the environment, the eggs embryonate (3) and become infective, containing the third-stage larva (4). Once ingested by the bovine host, the larva is released from the egg in the forestomach (5); subsequent development depends on the animal's age (adult cattle or calves). In adult cattle (black arrows), the larvae undergo somatic or visceral migration, thus reaching several organs and tissues, e.g. liver (6), heart (7), lungs (8), skeletal muscles (9) and udder (10), where they become latent. In pregnant cattle, the latent larvae become mobilised and migrate through the circulation and the placenta to the liver of the fetus (11). After the birth of the calves (dashed green arrows), the larvae migrate from the liver (6) to the heart (7) and lungs (8), where they moult to fourth-stage larvae and, via the trachea, travel up the respiratory system where they are swallowed and reach the intestine. Here they develop to adult nematodes (1). Calves can acquire the infection through their mother's colostrum and milk, as somatic larvae that become mobilised during pregnancy can be excreted via the udder (10, 12). In the case of transmammary infection, larval migration does not occur and the parasites develop into adults in the intestine within 20–23 days.



Toxascaris

Large worms grossly very similar to *Toxocara canis* with cervical alae present. A posterior bulb is absent from the oesophagus. The tail of the male does not possess a narrow terminal appendage as is the case for *T. canis* and *T. mystax*. The main species is *Toxascaris leonina* (syn. *Toxascaris limbata*) which infects the small intestine of dogs, cats, foxes, wild canids and felids.

Toxascaris leonina

Synonym: *Toxascaris limbata*

Description: Males measure up to 7 cm and females up to 10 cm long. Adults have an elliptical head due to the presence of cervical alae, which are slender and arrow-like, and taper posteriorly (Fig. 1.66b). Three large lips surround the mouth, there is no buccal capsule and the oesophagus lacks a bulb. The tail of the male is simple. The female genital organs lie behind the level of the vulva. The egg is slightly ovoid, with a smooth, thick, almost colourless shell. The yellowish-brown granular unsegmented contents fill only part of the shell. Eggs measure about 75–85 by 60–70 µm and are characteristic in dog and cat faeces.

Life cycle: The infective stage is the egg containing a second-stage larva or the third-stage larvae present in a mouse intermediate host. The eggs develop rapidly to the infective stage (about one week) compared with that for *Toxocara* species (around four weeks). Following ingestion and hatching, larvae enter the wall of the small intestine and remain for about two weeks. No migration of larvae occurs, as with other ascarid species. Third-stage larvae appear after about 11 days and moult to L_4 about 3–5 weeks post infection. Adult stages appear from about six weeks post infection and lie in the lumen of the intestine. The prepatent period is 10–11 weeks.

Parascaris

This very large, rigid, stout, whitish nematode, up to 40 cm in length, is found in the small intestine of equids (Fig. 1.67).

Life cycle: The life cycle is direct and migratory, involving a hepatopulmonary route. Eggs produced by the adult female worms are passed in the faeces and can reach the infective stage containing the L_2 in as little as 10–14 days, although development may be delayed at low temperatures. After ingestion and hatching, the larvae penetrate the intestinal wall and within 48 hours have reached the liver. By two weeks, they have arrived in the lungs where they migrate up the bronchi and trachea, are swallowed and return to the small intestine. The site of occurrence and timing of the parasitic larval moults of *P. equorum* are not precisely known, but it would appear that the moult from L_2 to L_3 occurs between the intestinal mucosa and the liver and the two subsequent moults occur in the small intestine. The minimum prepatent period of *P. equorum* is 10 weeks; longevity is up to two years. There is no evidence of prenatal infection. The main species is *Parascaris equorum* (syn. *Ascaris equorum*, *Ascaris megacephala*) which infects the small intestine of horses, donkeys and zebras.

Fig. 1.67 *Parascaris equorum* adult worms in the small intestine.

Parascaris equorum

Description: This very large, rigid, stout, whitish nematode cannot be confused with any other intestinal parasite of equines. Males measure 15–25 cm and females up to 40–50 cm in length. The adult parasites have a simple mouth opening surrounded by three large lips, and in the male the tail has small caudal alae. The dorsal lip has two double papillae and each ventrolateral lip has one double subventral and a small lateral papilla. Spicules are long and stout. The medium-sized egg of *P. equorum* is almost spherical (85–100 × 80–90 µm), brownish and thick-shelled with an outer pitted albuminous coat.

Porrocaecum

Species of this genus are parasites of a range of birds and various fish-eating mammals.

Life cycle: Similar to other ascarid species. The main species is *Porrocaecum crassum* which infects the small intestine of ducks. This parasite has earthworms as intermediate hosts.

Porrocaecum crassum

Description: The worms are reddish-white in colour, males measuring 12–30 mm and females 40–55 mm in length. Caudal alae are absent. The tail of the male is conical.

Bayliascaris

Species of the genus *Bayliascaris* are found in a wide range of mammal hosts. *Bayliascaris procyonis*, whose defintive host is the raccoon, is of veterinary importance because it has the ability to infect a wide range of wild and domestic animals and occasionally humans, causing visceral *larva migrans*.

Life cycle: The definitive hosts for this parasite are mammals such as skunks and raccoons, in which the nematode localises in the small intestine, eliminating eggs out in the faeces. These eggs can remain viable in the environment for several years. When ingested by paratenic hosts (e.g. dogs, cats, rodents, lagomorphs, gallinaceous birds, ostriches and occasionally humans), the larvae develop and penetrate into the circulation and eventually enter the brain and spinal cord.

Bayliascaris procyonis

Description: Adult worms in the definitive host are whitish in colour, and measure 15–20 cm in length and 1 cm in width.

FAMILY ASCARIDIIDAE

Ascaridia

The worms (Table 1.29) are stout and densely white; male worms are 50–75 mm and female worms 70–120 mm long (Fig. 1.68). *Ascaridia* is by far the largest nematode of poultry.

Life cycle: The egg becomes infective at optimal temperatures in a minimum of three weeks and the parasitic phase is non-migratory, consisting of a transient histotrophic phase in the intestinal mucosa after which the adult parasites inhabit the lumen of the intestine. The egg is sometimes ingested by earthworms, which may act as transport hosts. Eggs can remain viable for several months under moist cool conditions but are killed by a dry hot environment. The prepatent period ranges from 4–6 weeks in chicks to eight weeks or more in adult birds. The worms live for about one year.

Ascaridia galli

Synonyms: *Ascardia lineata*, *Ascaridia perspicillum*

Description: Male worms are 50–75 mm and female worms 70–120 mm long. The anterior end is characterised by a prominent mouth, which is surrounded by three large trilobed lips. The edges of the lips bear teeth-like denticles. A posterior bulb is absent from the oesophagus. The tail of the male possesses small alae and also bears 10 pairs of papillae. Spicules are almost equal in length. In the male, there is a circular precloacal sucker, which has a thick cuticular rim. The medium-sized pale-brown egg is distinctly oval, with barrel-shaped side walls, and they are unsegmented when laid (see Fig. 4.8). They measure about 75–80 by 45–50 µm. The smooth thick shell has three layers, the middle one being more prominent. Eggs cannot easily be distinguished from those of the other common poultry ascaridoid, *Heterakis*.

Table 1.29 *Ascaridia* species.

Species	Hosts	Site
Ascaridia galli (syn. *Ascaridia lineata*, *Ascaridia perspicillum*)	Chickens, turkeys, geese, ducks, guinea fowl and a number of wild galliform birds	Small intestine
Ascaridia dissimilis	Turkeys	Small intestine
Ascaridia columbae (syn. *Ascaridia maculosa*)	Pigeons	Small intestine

Fig. 1.68 *Ascaridia galli* adult worms in the small intestine.

Ascaridia dissimilis

Description: The worms are stout and densely white. Males measure 35–50 mm and females 50–75 mm in length. The males of this species and those of *A. galli* are separated by differences in the position of the first and fourth pairs of ventral caudal papillae, and by the form of the spicules. The egg is distinctly oval, with a smooth shell, and is 80–95 µm in size.

Ascaridia columbae

Synonym: *Ascardia maculosa*

Description: The worms are stout and densely white; males are 16–70 mm and females 20–95 mm in length. The egg is distinctly oval, with a smooth shell, and measures 80–90 by 40–50 µm.

FAMILY HETERAKIIDAE

Heterakis

These are small to medium whitish worms up to 1.5 cm long, with elongated pointed tails (Table 1.30). Gross examination readily indicates the genus but for specific identification, microscopic examination is necessary to determine the shape of the oesophagus (in *Heterakis* the oesophagus has a large posterior bulb) and the size and shape of spicules. A buccal capsule is absent. Generic identity may be confirmed by the presence of a large, chitinous, circular precloacal sucker in the male and prominent caudal alae supported by 12 pairs of caudal papillae (Fig. 1.69). The precloacal sucker is much less prominent in *Ascaridia*.

Life cycle: The direct life cycle is similar to that of *Ascaridia* spp. The egg is infective on the ground in about two weeks at optimal temperatures. Eggs may remain viable in the soil for several months. Earthworms may be transport hosts, the eggs simply passing through

Table 1.30 *Heterakis* species.

Species	Hosts	Site
Heterakis gallinarum (syn. *Heterakis papillosa*, *Heterakis gallinae*, *Heterakis vesicularis*)	Chickens, turkeys, pigeons, pheasants, partridges, grouse, quails, guinea fowl, ducks, geese and a number of wild galliform birds	Caeca
Heterakis isolonche	Pheasants, grouse, quails, ducks, chickens	Caeca
Heterakis dispar	Ducks, geese, chickens	Caeca
Heterakis brevispeculum	Ducks, geese, guinea fowl, chickens	Caeca

Fig. 1.69 Adult *Heterakis gallinarum* worms.

the gut, or paratenic hosts in which the egg hatches and the L_3 travel to the tissues to await ingestion by the fowl. The prepatent period of the genus is about four weeks. Longevity is about 12 months.

Heterakis gallinarum

Description: The male is 7–13 mm long and the female 10–15 mm (Fig. 1.70). Gross examination readily indicates the genus but for specific identification, microscopic examination is necessary to determine the shape of the oesophagus and the size and shape of spicules. The oesophagus has a large posterior bulb. Generic identity may be confirmed by the presence of a large circular precloacal sucker in the male and prominent caudal alae supported by 12 pairs of caudal papillae (Fig. 1.70). The spicules are unequal in length, the left (about 0.7 mm) has broad alae and the right is slender (about 2 mm). The egg is ovoid, thick and smooth-shelled with almost parallel side walls (see Fig. 4.8). Eggs measure 65–80 by 35–46 µm and are unsegmented when laid. *Heterakis* eggs are sometimes difficult to distinguish from those of *Ascaridia*, although in the latter species the eggs are larger and have slightly barrel-shaped side walls.

Fig. 1.70 Tail of male *Heterakis gallinarum* showing prominent caudal alae supported by 12 pairs of caudal papillae. (Courtesy of Georgiana Deak).

Heterakis isolonche

Description: Male worms measure about 7–13 mm and females 10–15 mm in length. The spicules are long and of equal length. The spicules are asymmetrical and generic identity may be confirmed by the presence of a large circular precloacal sucker in the male and prominent caudal alae supported by large caudal papillae. The egg is ovoid, thick and smooth-shelled, about 65–75 by 38–45 µm. More details of the eggs are given under *H. gallinarum*.

Heterakis dispar

Description: Worms are larger than the other species, with males measuring 11–18 mm and females 16–23 mm in length. The spicules are short and equal in length (40–50 µm).

Heterakis brevispeculum

Description: The spicules are of equal length (about 0.5 mm) and possess a barb near the tip.

Other ascarids (Table 1.31) found in reptiles are briefly mentioned and covered in Chapter 16. Members of the genera *Ophidascaris* and *Polydelphus* are mainly parasites of snakes and lizards, occasionally of amphibians. *Angusticaecum* spp. are ascarids of tortoises.

Table 1.31 Reptilian ascarid species.

Species	Hosts	Site
Ophidascaris spp.	Snakes, lizards	Intestine
Polydelphus spp.	Snakes	Intestine
Angusticaecum holopterum	Reptiles (chelonia)	Intestine

FAMILY ANISAKIDAE

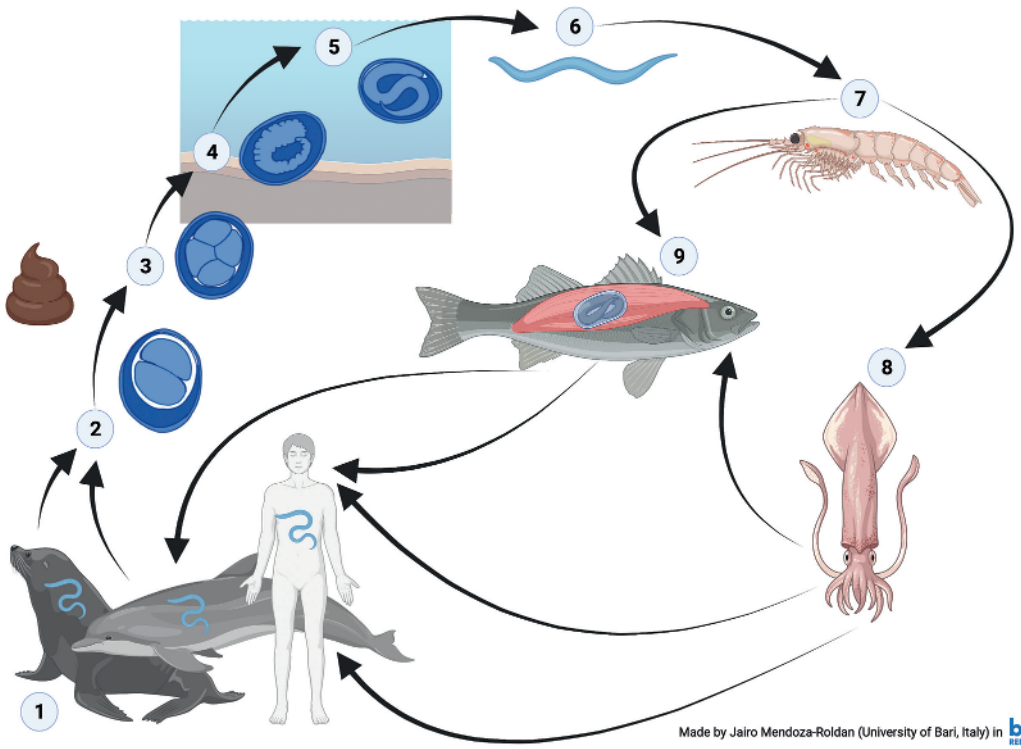
Members of the Anisakidae (Table 1.32) have life cycles involving marine mammals and fish and are of importance mainly in human medicine as some species can cause disease through the ingestion of raw or uncooked fish. Detailed descriptions are not within the scope of this book. See **life cycle 11**.

Table 1.32 Anisakidae species.

Species	Final hosts	Site	Intermediate hosts
Anisakis simplex	Whales, dolphins, seals	Stomach and intestine	Crustaceans, fishes
Contracaecum spiculigerum	Ducks, geese, swans, waterfowl	Small intestine	Invertebrates (copepods, crustaceans, insects, etc.) Damselflies, fishes, tadpoles
Contracaecum spp.	Whales, dolphins, seals	Stomach and intestine	Copepods, fishes
Pseudoterranova decipiens (syn. *Phocanema decipiens*)	Seals	Stomach	Crustaceans, fishes
Sulcascaris spp.	Reptiles (turtles)	Intestine	Molluscs

LIFE CYCLE 11. LIFE CYCLE OF *ANISAKIS* SPP.

Anisakis spp. are nematode parasites of several animal species, including humans. Adult *Anisakis* live in the intestine of fishes and sea mammals. The unembryonated eggs (2) reach the marine environment via the host faeces. Following embryonation (3), formation of first- (L_1) (4) and second-stage larvae (L_2) (5) occurs inside the egg, which subsequently hatches, releasing the L_2 (6). The L_2 are ingested by small marine crustaceans (7) and invade the host haemocoel where they moult to third-stage larvae (L_3). Once infected crustaceans are eaten by cephalopods (8) or predatory fish (9), the larvae migrate from the intestinal tract of the new host to the coelomatic cavity, where they encapsulate on the surface of organs and skeletal muscles (particularly following the death of the host). Predatory fish (9) represent a key element of the life cycle, as these hosts accumulate and transmit larvae ingested by infected fish, crustaceans and cephalopods. The definitive host acquires the infection via ingestion of infected fish or cephalopods. In humans, the larvae present in raw or undercooked fish may migrate through the intestinal mucosa or other tissues.



FAMILY ASPIDODERIDAE

Paraspidodera

The main species is *Paraspidodera uncinata* which infects the large intestine of guinea pigs.

Paraspidodera uncinata

Description: Male worms are 16–17 mm and females 18–21 mm in length. Both sexes have a large bulb-shaped oesophagus. Caudal alae are absent. The male spicules are of equal length. The male has a precloacal sucker. The egg is small, ellipsoidal and measures about 43 by 31 µm. The shell is thick with a smooth surface and the contents are unsegmented.

SUPERFAMILY SUBULUROIDEA

Members of this superfamily are parasites mainly of rodents and are characterised by weakly developed lips with sensilla and a thick-walled stoma that is armed with three teeth. The only genus of veterinary importance is *Subulura*, species of which are parasites of poultry.

FAMILY SUBULIRIDAE

Subulura

Species of this genus, found in birds, are small worms located in the caecae. They are similar to *Heterakis*, although the tail is not as pointed. The males measure around 8–10 mm and the females up to 14–18 mm in length.

Life cycle: Eggs passed in faeces are ingested by the intermediate host where they develop to the infective L_3 stage after about two weeks. Following ingestion by the final host, the larvae migrate to the lumen of the caeca. The prepatent period is 6–8 weeks. The main species is *Subulura suctoria* (syn. *Subulura brumpti*, *Subulura differens*, *Allodapa suctoria*) which infects the caeca of chickens, turkeys, guinea fowl, quails, grouse, pheasants and ducks. This parasite has beetles and cockroaches as intermediate hosts.

Subulura suctoria

Synonyms: *Subulura brumpti*, *Subulura differens*, *Allodapa suctoria*

Description: The buccal capsule is small and possesses three teeth at its base. The oesophagus is dilated posteriorly, followed by a bulb. The tail of the male has large lateral alae and is curved ventrally. Two long thin curved spicules are present. A slit-like precloacal sucker is present, surrounded by radiating muscle fibres. In the female, the vulva is situated just anterior to the middle of the body.

ORDER OXYURIDA

SUPERFAMILY OXYUROIDEA

Adult oxyuroids of animals inhabit the large intestine and are commonly called 'Pinworms' because of the long pointed tail of the female parasite. The ventrolateral papillae are often absent and where present are very much reduced. The number of spicules can vary in the males from zero, one or two depending on the species. They have a double bulb oesophagus, the posterior bulb being well developed. The life cycle is direct. The genera of veterinary interest are *Oxyuris* and *Probstmayria*, both parasitic in the horse; *Skrjabinema*, which are parasites of ruminants; *Syphacia* and *Aspiculuris* found in rodents; *Passalurus* and *Dermatoxys* found in rabbits and hares; and *Tachygonetria* found in reptiles. Oxyurids also include the common human pinworm, *Enterobius*.

FAMILY OXYURIDAE

Oxyuris

The adult female worms, which may reach 10–15 cm in length, are found in the lumen of the caecum and large colon of equids. The much smaller males are difficult to observe in digesta. The main species is *Oxyuris equi* and infects the caecum, colon and rectum of horses and donkeys.

Life cycle: The life cycle is direct. The adult worms are found in the lumen of the caecum and the small and large colon. After fertilisation, the gravid female migrates to the anus, extrudes her anterior end and lays her eggs in clumps (up to 50 000 eggs per female), seen grossly as yellowish-white gelatinous streaks on the perineal skin or perianal region. Development is rapid and within 4–5 days the egg contains the infective L_3. Eggs are rubbed off and contaminate the environment. Infection is by ingestion of embryonated eggs on fodder, grass, bedding, etc. The larvae are released in the small intestine, move into the large intestine and migrate into the mucosal crypts of the caecum and colon where development to L_4 takes place within 10 days. The L_4 then emerge and feed on the mucosa before maturing to adult stages that inhabit the lumen and feed on intestinal contents. The prepatent period of *O. equi* is about five months. Longevity of female worms is around six months.

Oxyuris equi

Description: The mature females are large, greyish-white, opaque worms with very long tapering tails that may reach 10–15 cm in length, whereas the mature males are generally less than 1.2 cm long (Fig. 1.71). *Oxyuris equi* L_4 are 5–10 mm in length, have long tapering tails and are often attached orally to the intestinal mucosa. There is a double oesophageal bulb (Fig. 1.72; see also Fig. 1.3) and the tiny males have caudal alae and a single pin-shaped spicule. In the female the vulva is situated anteriorly. *Oxyuris equi* eggs are ovoid, yellowish, thick-shelled, smooth and slightly flattened on one side with a transparent mucoid operculate plug at one end (see Fig. 4.5). Eggs measure 80–95 by 40–45 µm and contain a late-stage morula or a first larval stage when shed in faeces.

Skrjabinema

Skrjabinema are small non-pathogenic pinworms in the caecum of domestic and wild ruminants (Table 1.33).

Life cycle: The life cycle is direct. Embryonated eggs are deposited on the perineal skin by the adult female worms. Infection is by ingestion of the embryonated egg.

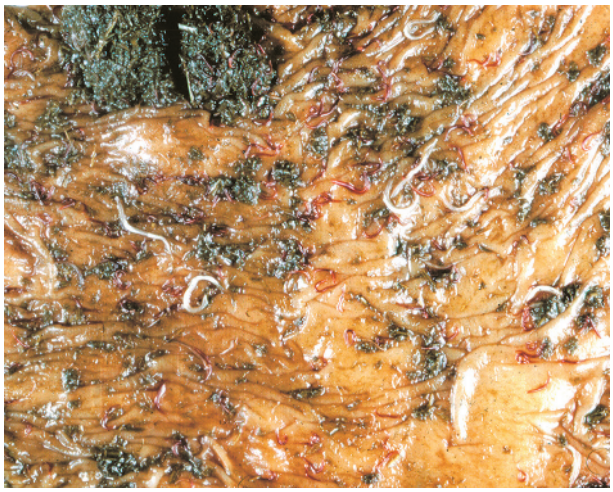


Fig. 1.71 Mixed infection of *Oxyuris equi* adults (white) and small strongyles in the colon.

Fig. 1.72 Head of *Oxyuris equi* with double oesophageal bulb.

Table 1.33 *Skrjabinema* species.

Species	Hosts	Site
Skrjabinema ovis (syn. *Oxyuris ovis*)	Goats, sheep	Caecum, colon
Skrjabinema alata	Sheep	Caecum, colon
Skrjabinema caprae	Goats	Caecum, colon
Skrjabinema parva	Deer (white-tailed)	Caecum, colon

Skrjabinema ovis

Description: Small worms, up to 7 mm in size; male are around 3 mm and females 6–7 mm in length. There are three large intricate lips and three small intermediate lips. The oesophagus is cylindrical in cross-section and ends in a large spherical bulb. The male worm has a single spicule and the tail is rounded with a cuticular expansion supported by two pairs of processes. Eggs are asymmetrically flattened, larvated and measure 55–60 by 32–35 µm.

Life cycle: The prepatent period for this species is about 25 days.

Aspicularis

These are small pinworms of rodents. Males are 2–4 mm and females 3–4 mm long.

Life cycle: The life cycle is direct. Females deposit embryonated eggs on the perineal skin. Infection occurs in three ways:

1 directly by ingestion of embryonated eggs from the perineum
2 indirectly with food
3 by retro-infection when eggs hatch in the perineal region and migrate back via the anus.

The main species is *Aspicularis tetraptera* which infects the caecum and colon of mice and rats.

Aspicularis tetraptera

Description: The oesophageal bulb is oval, the oesophagus is club-shaped and the mouth has three lips. The cervical alae are broad and their posterior margin ends abruptly. There is no spicule or gubernaculum in the male.

Syphacia

These are small whitish worms, up to 6 mm in size, localised in the caecum and colon of mice and rats. Males measure 1–1.5 mm and females 3.4–6 mm. The mouth has three distinct lips without a buccal capsule. The oesophagus has a prebulbular swelling and a posterior globular bulb. Small cervical alae, with rounded posterior margins, are present. The males have a single long slender spicule.

Syphacia obvelata

Description: The adult male is 1.1–1.6 mm long and 125 µm wide with the tail length about equal to its body width. Female worms measure 3.4–5 mm in length.

Syphacia muris

Description: The adult male is 1.2–1.3 mm long and 100 µm wide and the tail length is about twice the body width. The females measure 2.8–3.4 mm in length. The vulva of *S. muris* is further posterior, in relation to the oesophageal bulb, than that of *S. obvelata*.

Passalurus

Species of *Passalurus* are common pinworms localised in the caecum and colon of rabbits and hares.

Life cycle: Development is direct and infection occurs through the ingestion of infective eggs. Immature stages are found in the mucosa of the small intestine and caecum.

Passalurus ambiguus

Description: Adult worms are 4–11 mm in size and semi-transparent; males are 4–5 mm and females 9–11 mm. The oesophagus has the

typical oxyurid oesophageal bulb. The distal extremity of the female tail possesses around 40 circular striations. The male spicule is simple in appearance and the tail has an appendix shaped like a whip. Eggs are thin-walled, with slightly flattened walls on one side and measure 95–103 by 43 µm.

Dermatoxys

Species of *Dermatoxys* are common pinworms of rabbits and hares.

Life cycle: Details of the life cycle are not known. It is probably direct and similar to other pinworms. The main species is *Dermatoxys veligera* which infects the caecum and colon of rabbits and hares.

Dermatoxys veligera

Description: Female worms are 16–17 mm and males 8–11 mm long. Males have small spicules. Females have a vulva located in the cranial half of their body.

Enterobius

This genus includes the human pinworm, *Enterobius vermicularis*, which is also found in apes, and *Enterobius anthropopitheci* of chimpazees. Both are found in the caecum and colon.

Life cycle: Gravid female worms in the caecum and colon migrate to the rectum and deposit eggs on the perineum. Eggs become infective within a few days and infection is via the embyonated egg. The prepatent period is about eight weeks.

Enterobius vermicularis

Description: Adults are slender cream-coloured worms with long tails. Males measure 2–5 mm and females 8–13 mm in length.

FAMILY KATHLANIIDAE

Probstmayria

Small, slender, viviparous nematodes that are perpetual parasites, living from generation to generation in the equine large intestine. The main species is *Probstmayria vivipara* which infects the colon of horses.

Probstmayria vivipara

Description: Adult worms are 2–3 mm long with long filamentous tails. The mouth has six small lips and the buccal capsule is cylindrical and long. The oesophagus has an expanded posterior bulb. A large sucker-like excretory pore is present. The tail of the male is curved into a hook shape.

Life cycle: *Probstmayria vivipara* is unusual in that it is a perpetual parasite and lives from generation to generation in the equine caecum and colon. The females are viviparous and give birth to larvae almost as large as the adults. Both adults and larvae may be passed in the faeces.

FAMILY PHARYNGODONIDAE

The Pharyngodonidae includes a number of genera that are pinworms of reptiles. The genus *Tachygonetria* is commonly found in Mediterranean tortoises (*Testudo* spp.).

ORDER SPIRURIDA

SUPERFAMILY SPIRUROIDEA

The precise classification of a number of genera currently assigned to this superfamily is controversial, but there are some of significance in veterinary medicine: *Spirocerca*, *Habronema*, *Draschia*, *Parabronema*, *Thelazia*, *Gnathostoma*, *Gongylonema* and to a lesser extent *Ascarops*, *Physocephalus*, *Simondsia*, *Physaloptera*, *Spirura*, *Odontospirura*, *Tetrameres*, *Histiocephalus*, *Hartertia*, *Oxyspirura*, *Metathalazia* and *Vogeloides*. A major characteristic of this group is the tight, spirally coiled tail of the male. The life cycles are indirect, involving arthropod intermediate hosts.

Members of the genus *Thelazia* are principally found in or around the eyes of animals and can be responsible for keratitis. Unlike most spiruroids, the L_1 stage is not ingested from the faeces but by flies feeding on ocular secretions.

The genus *Gongylonema* is unusual among the spiruroids in having a very wide final host range, which includes all the domesticated animals, though it is most prevalent in ruminants. Like most spiruroids, the favoured location of the adults is the upper alimentary tract, the oesophagus and the forestomachs and stomach of mammals and the crop of birds. Species belonging to the genera *Cheilospirura*, *Echinuria*, *Dispharynx* and *Streptocara* are now considered to be members of the superfamily Acuarioidea.

FAMILY SPIROCERCIDAE

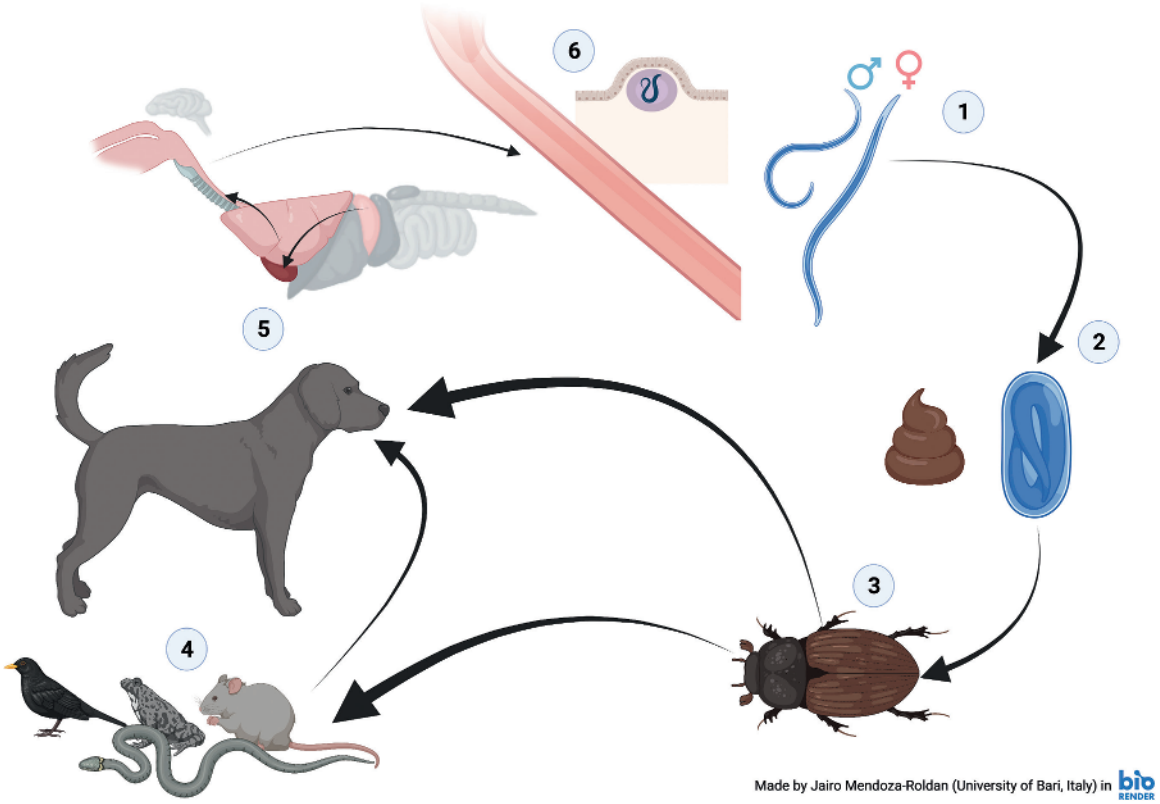
Spirocerca

These are stout, reddish, spirally coiled worms, 3–8 cm long, are found in tumour-like granulomas in the wall of the oesophagus and stomach.

Life cycle: The thick-shelled elongate egg containing a larva is passed in the faeces or vomit, and does not hatch until ingested by a dung beetle. In this, the intermediate host, the larva develops to the L_3 and encysts. Paratenic hosts may also be involved if the dung beetle, in turn, is ingested by any of a variety of other animals including the domestic chicken, wild birds and lizards. In these, the L_3 become encysted in the viscera. On ingestion of the intermediate or paratenic host by the final host, the L_3 are liberated, penetrate the stomach wall and migrate via the coeliac artery to the thoracic aorta. About three months later, the majority of larvae cross to the adjacent oesophagus where they provoke the development of granulomas as they develop to the adult stage in a further three months. Adults are usually located in cystic nodules which communicate with the lumen of the stomach or oesophagus through fistulae. The prepatent period is therefore about 5–6 months. Eggs, however, may not be found in the faeces of a proportion of animals with adult infections where the granulomas have no openings into the oesophageal lumen. The main species is *Spirocera lupi* which infects the oesophagus, stomach and aorta of dogs, foxes, wild canids, occasionally cats and wild felids. This parasite has coprophagous beetles as intermediate hosts. See **life cycle 12**.

LIFE CYCLE 12. LIFE CYCLE OF *SPIROCERCA LUPI*

Adults of *Spirocerca lupi* (1) live in nodules that develop within the wall of the thoracic section of the oesophagus of dogs and other canids, which act as definitive hosts. Adult females release larvated eggs (2) that reach the oesophageal lumen through a round opening of the nodule (nipple-like) and are excreted in the environment with the faeces or emesis. The life cycle continues when eggs are ingested by free-living biological vectors (coprophagous Coleoptera) (3) that act as intermediate hosts; within these hosts, the parasites develop into infective third-stage larvae. Other animals, such as amphibians, reptiles and birds, may act as paratenic hosts (4), harbouring live infective larvae. The dog acquires the infection by ingesting intermediate or paratenic hosts harbouring infective larvae of *S. lupi*. After ingestion, the larvae penetrate the gastric wall and, via the coeliac artery, migrate to the thoracic aorta and subsequently to the oesophageal wall (5, 6) where they moult and develop into sexually mature adults ~6 months after initial infection.



Spirocerca lupi

Description: Adult worms are spirally coiled and have a blood-red colour; males are around 30–55 mm and females 55–80 mm. The lips are trilobed and the pharynx is short. The male tail bears lateral alae (four pairs and one unpaired), median precloacal papillae and two pairs of postcloacal papillae, with a group of minute papillae near the tail tip. The very small eggs have smooth thick shells and are elongate with parallel side walls. They measure about 30–37 by 11–15 µm and are larvated when passed in faeces.

Ascarops

Worms of this genus, and of the genera *Physocephalus* and *Simondsia*, live on the stomach wall of pigs and wild boar under a layer of mucus, and occasionally in the small intestine.

Life cycle: The life cycle is typically spiruroid. Eggs passed in the faeces of the infected host develop into infective larvae, if ingested by coprophagous beetles. The life cycle is completed when pigs ingest the beetles. The prepatent period is about four weeks.

Ascarops strongylina

Synonym: *Arduenna strongylina*

Description: Small slender filiform worms, the males measuring up to 15 mm and the reddish females about 22 mm long. A cervical ala is located only on the left side of the body. The wall of the pharynx contains several spiral supports and a small tooth is present on each of the two lips. The right caudal alae in the male are much larger than the left and there are four pairs of asymmetrical precloacal papillae and one pair of caudal papillae. The left spicule is about 4–5 times longer than the right spicule. Eggs are small, thick-shelled, 34–39 by 20–22 µm, and are embryonated when passed.

Ascarops dentata

Synonym: *Arduenna dentata*

Description: Similar to *A. strongylina* but much bigger; male worms are 35 mm and female worms are 55 mm long. The buccal capsule has two teeth anteriorly.

Physocephalus

Small slender worms found on the surface of the stomach wall.

Life cycle: The life cycle is typically spiruroid. Eggs passed in the faeces of the infected host develop into infective larvae, if ingested by coprophagous beetles. The prepatent period is about six weeks. The main species is *Physocephalus sexalatus* which infects the stomach of pigs and camels, rarely rabbits and hares. This parasite has coprophagous beetles as intermediate hosts.

Physocephalus sexalatus

Description: Small slender filiform worms which are reddish when fresh, the males measuring about 10–12 mm and the females up to 22 mm long. The anterior of the body is thinner than the posterior region and just posterior to the vestibule is a cuticular swelling. There are three cervical alae on either side and the cervical papillae are asymmetrically located. The wall of the pharynx contains a single spiral support. In the male worm, the caudal alae are narrow and symmetrical and there are four pairs of precloacal papillae. The left spicule is about 6–7 times longer than the right spicule. Eggs are small, an elongated ellipse, thick-shelled, measure around 34–39 by 15–17 µm and are embryonated when passed.

Simondsia

Male worms live on the surface of the gastric mucosa, but the females are found in small cysts in the mucosal crypts with their anterior ends protruding.

Life cycle: The life cycle is indirect. Eggs are passed in the faeces and ingested by beetles in which they hatch and develop to infective larvae. The parasites continue development when the intermediate host is ingested by a pig. The main species is *Simondsia paradoxa* (syn. *Spiroptera cesticillus*) which infects the stomach of pigs, rarely rabbits and hares. This parasite has coprophagous beetles as intermediate hosts.

Simondsia paradoxa

Synonym: *Spiroptera cesticillus*

Description: The males are small slender worms measuring about 12–15 mm in length and possess a spirally coiled tail. Female worms measure up to about 15–20 mm in length. They have large lateral alae and a large ventral and dorsal tooth. The gravid female has a characteristic form, the posterior end of the body being a rounded sac filled with eggs and the anterior end is slender. The small eggs are oval or ellipsoid, 20–29 µm, and are embryonated when laid.

Table 1.34 *Streptopharagus* species.

Species	Hosts	Site	Intermediate hosts
Streptopharagus armatus	Rhesus monkeys, cynomolgus monkeys, Japanese macaques, guenons, baboons, gibbons	Stomach	Coprophagous beetles
Streptopharagus pigmenatus	Rhesus monkeys, cynomolgus monkeys, Japanese macaques, guenons, baboons, gibbons	Stomach	Coprophagous beetles

Streptopharagus

Worms of this genus are found in the stomachs of Old World monkeys and apes (Table 1.34).

FAMILY HABRONEMATIDAE

Habronema

Members of the genus *Habronema* are small, slender, white translucent worms 1.5–2.5 cm long (Fig. 1.73). The male has wide caudal alae and the tail has a spiral twist. Together with the closely related genus *Draschia*, they are parasitic in the stomach of the horse. *Habronema* inhabits the mucus layer of the gastric mucosa and may cause a catarrhal gastritis, but is not considered an important pathogen. The chief importance of these parasites is as a cause of cutaneous habronematidosis or 'summer sores' in warm countries.

Life cycle: The life cycle is similar for all species. Eggs or L_1 are passed in the faeces and the L_1 are ingested by the larval stages of various muscid flies of the genera *Musca*, *Stomoxys* and *Haematobia* (*Lyperosia*), that are often present in faeces. Development to L_3 occurs synchronously with the development to maturity of the fly intermediate host. When the fly feeds around the mouth, lips, ocular conjunctiva and nostrils of the horse, the larvae pass from its mouthparts onto the skin and are swallowed. Alternatively, infected flies may be swallowed whole in feed and drinking water. Development to adult takes place in the stomach where the larvae burrow into the glandular area of the mucosa and induce the formation of nodules. The worms develop to mature adults within the nodules in about eight weeks. When the larvae are deposited on a skin wound or around the eyes, they can invade the tissues; they do not complete their development but may cause granulomatous skin lesions. See **life cycle 13**.

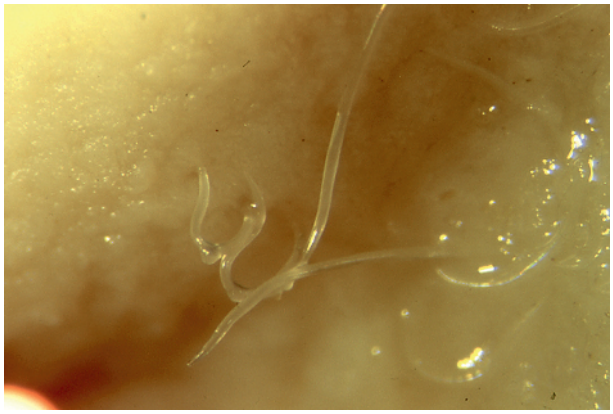
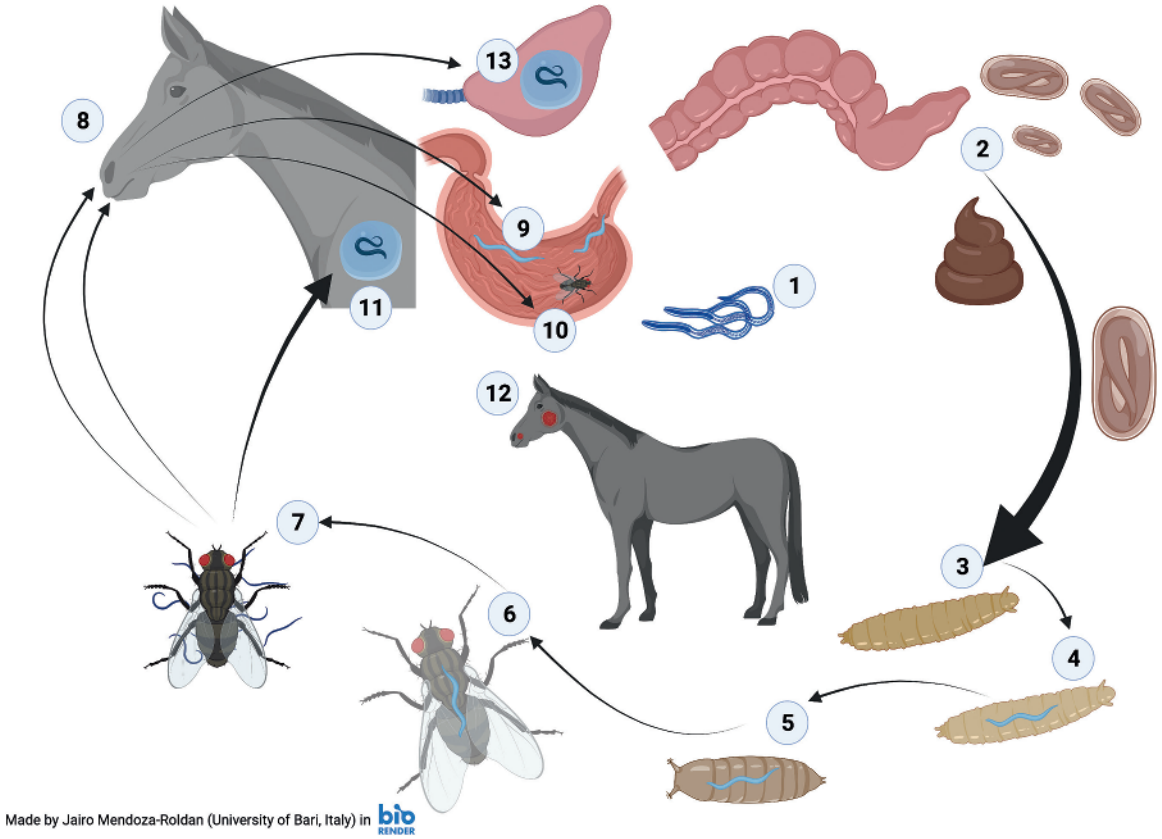


Fig. 1.73 Adult *Habronema* worms.

LIFE CYCLE 13. LIFE CYCLE OF *HABRONEMA MUSCAE*, *HABRONEMA MICROSTOMA* AND *DRASCHIA MEGASTOMA*

The adults of *Habronema muscae*, *Habronema microstoma* and *Draschia megastoma* live in the stomach (1) and, after mating, the females release larvated eggs, a proportion of which hatch during transit through the gastrointestinal tract, thus freeing the L_1, with the remainder excreted with the faeces and hatching in the external environment (2). The life cycle requires larval stages of flies that act as intermediate hosts. Briefly, fly larvae hatching from the eggs deposited on the host faecal pat (3) ingest the nematode larvae (4), and the development of the fly larvae occurs simultaneously to that of the nematodes (5), with adult flies harbouring infective third-stage larvae (L_3) (6). Infected flies, attracted by host secretions, land on the latter and release larvae of *Habronema* and *Draschia* (7). The larvae deposited near the lips and perilabial area (8) are swallowed, thus reaching the stomach (9) and developing to sexually mature adults within two months, completing the life cycle. Definitive hosts may also acquire the infection via ingestion of water and feedstuffs contaminated by infected flies (10). The larvae deposited on the skin (11), particularly on wounds and abrasions, cause cutaneous habronemiasis (12), while those deposited on the nasal mucosa can migrate to the lungs and establish in the bronchioles and alveoli, causing pulmonary habronemiasis (13).



Habronema microstoma

Description: Adult males are 16–22 mm and females 15–25 mm long. The anterior region of the cylindrical pharynx contains a small dorsal and ventral tooth in its anterior region. Four pairs of precloacal papillae are present in the male worm. Spicules are uneven in length, with the left spicule (0.8 mm) being about twice as long as the right (0.4 mm). The buccal cavity is cylindrical in shape and the pharynx contains a dorsal and ventral tooth in its anterior part. The male has four pairs of precloacal papillae. Spicules are uneven in length, with the slender left one longer than the right. The very elongated, ellipsoidal, small eggs are thin-shelled, about 45–59 by 10–16 µm, and larvated when shed in faeces. Both eggs and larvae can be found in faeces. Eggs resemble those of *Draschia* but are slightly larger.

Habronema muscae

Description: Slender white translucent worms, 1–2.5 cm long; adult males are 8–14 mm and females 13–25 mm. The male has wide caudal alae and the tail has a spiral twist. It is unlikely to be confused with other nematodes in the stomach since *Draschia* is associated with characteristic lesions and *Trichostrongylus axei* is less than 1 cm in length. There are two lateral trilobed lips; the pharynx is cylindrical and has a thick cuticular lining. There are four pairs of precloacal papillae and one or two papillae behind the cloaca. The cloacal region is covered with small cuticlar ridges. Spicules are uneven in length, with the slender left one about five times longer than the right. The vulva is situated near the middle of the body and opens dorsolaterally. The elongated, oval, small eggs are thin-shelled, 40–50 by 10–12 µm, and larvated when shed in faeces. Eggs or larvae may be observed in the faeces.

Draschia

These worms are very similar to *Habronema* but smaller with a distinct collar in the anterior region. *Draschia* parasitises the fundic region of the stomach wall and provokes the formation of large fibrous nodules that are occasionally significant. The female worms are ovoviviparous. The main species is *Draschia megastoma* (syn. *Habronema megastoma*) which infects the stomach of horses and other equids. This parasite has dipteran flies, *Musca*, *Stomoxys* and *Haematobia* (*Lyperosia*) as intermediate hosts.

Draschia megastoma

Description: Slender white translucent worms 7–13 mm long; adult males are 7–10 mm and females 10–13 mm. The worms are recognised by their heads, which are slightly constricted from the main body by a deep groove which circles the body just posteriorly to the oral region (Fig. 1.74). The pharynx is funnel-shaped. Male worms have four pairs of precloacal papillae. The spicules are short and uneven in length with the left (0.5 mm) longer than the right (0.25 mm). The eggs are thin-shelled and elongate and measure around 35 by 8 µm and hatch in the stomach.

Parabronema

Parabronema are found in the abomasum of ruminants. The genus is readily distinguished from the other abomasal worms by the presence of large cuticular shields and cordons in the cephalic region.

Life cycle: Eggs or L_1 are passed in the faeces and the L_1 are ingested by the larval stages of various muscid flies that are often present in faeces. Development to L_3 occurs synchronously with the development to maturity of the fly intermediate host. When the fly feeds around the mouth, lips and nostrils of the host, the larvae pass from its mouthparts onto the skin and are swallowed. Alternatively, infected flies may be swallowed whole in feed and drinking water. Development to adult takes place in the glandular area of the abomasum. The main species is *Parabronema skrjabini* which infects the abomasum of sheep, goats, cattle and camels. This parasite has muscid flies of the genera *Stomoxys*, *Lyperosia* and *Haematobia* as intermediate hosts.

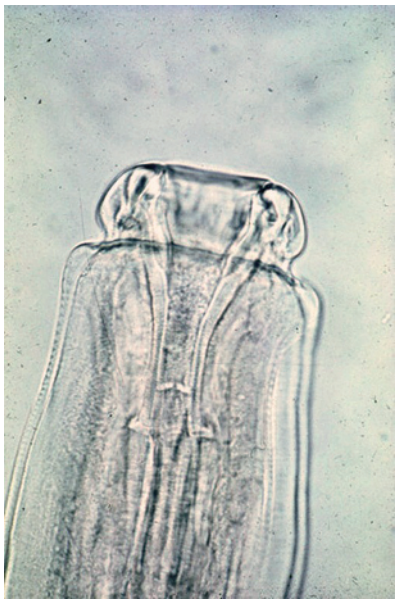


Fig. 1.74 Head of *Drachsia megastoma*.

Parabronema skrjabini

Description: The white slender adult worms (up to 3.6 cm long) resemble *Haemonchus* spp. somewhat in gross form and size, but without the red spiral coloration, while the younger worms are closer to *Ostertagia* in appearance. Males measure 15–18 mm with one spicule. The genus is readily distinguished from the other abomasal worms by the presence of large cuticular shields and cordons in the cephalic region. The tail of the male is spiral with four pairs of preanal papillae.

Histiocephalus

The main species is *Histiocephalus laticaudatus* which infects the gizzard of chickens and ducks. The intermediate host of this parasite is unknown.

Histiocephalus laticaudatus

Description: Males measure around 7–7.5 mm and females 13–16 mm in length. The mouth is surrounded by four lips and the pseudolips are indented, forming 10 finger-like expansions, each with two or three points. Adult worms have ornate leaf-like structures and a cervical collar. The buccal cavity is cylindrical. Males have two large alae and four pairs of precloacal papillae and two pairs of postcloacal papillae. Spicules are long and of equal length. A gubernaculum is absent. The vulva in the female is situated anteriorly.

Life cycle: Little is known of the life cycle.

FAMILY THELAZIDAE

Thelazia

Members of this genus are parasites of the conjunctival sac and lacrimal duct and because of their location are also known as 'eye-worms' (Table 1.35). Worms have a large vestibule and lips are absent in this genus. Prominent striations are present on the anterior cuticle. Caudal alae are absent in the male worms.

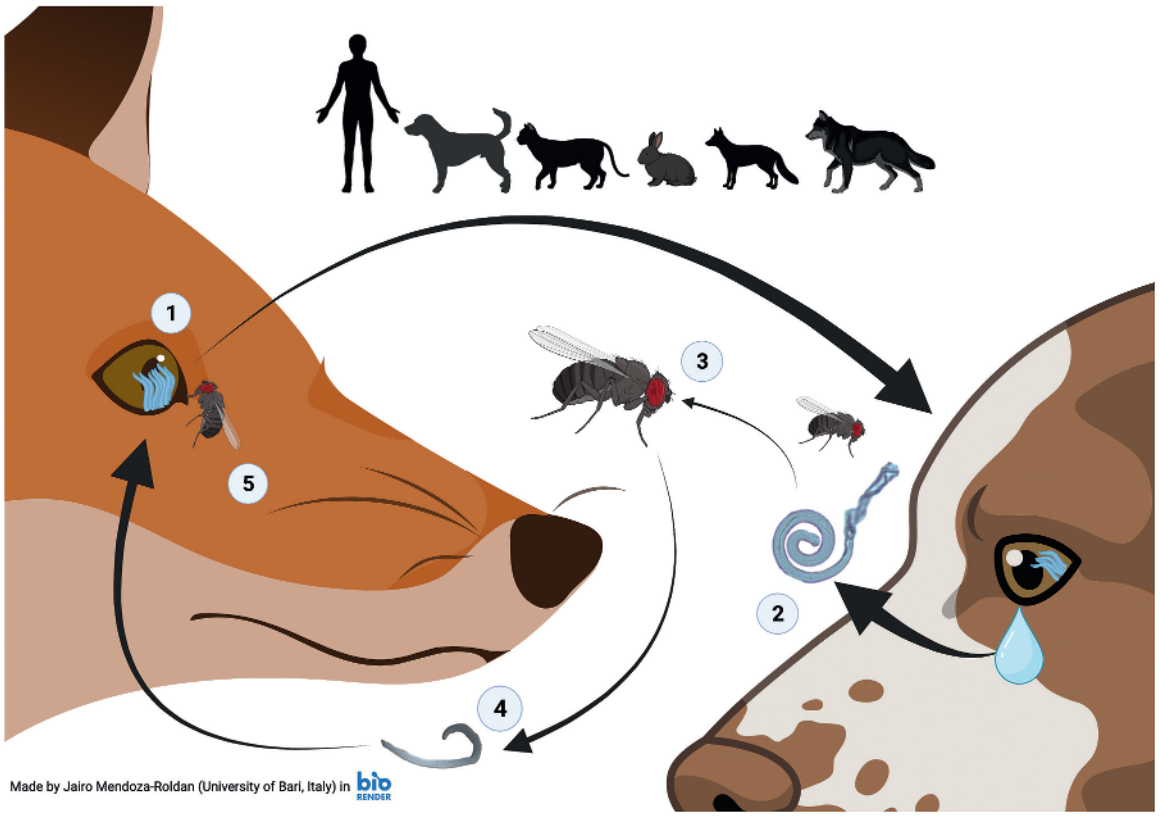
Life cycle: The worms are viviparous. The L_1 passed by the female worm into the lacrimal secretion are ingested by the fly intermediate host as it feeds. Development from L_1 to L_3 occurs in the ovarian follicles of the fly in 15–30 days during the summer months. L_3 migrate to the mouthparts of the fly and are transferred to the final host when the fly feeds. Development in the eye takes place without further migration. See **life cycle 14**.

Table 1.35 *Thelazia* species.

Species	Hosts	Site	Intermediate hosts
Thelazia rhodesi	Cattle, buffalo, occasionally sheep, goats, camels	Eye, conjunctival sac, lacrimal duct	Muscid flies, particularly *Fannia* spp.
Thelazia gulosa (syn. *Thelazia alfortensis*)	Cattle, sheep, wild ruminants	Eye, conjunctival sac, lacrimal duct	Muscid flies (*Musca* spp.)
Thelazia skrjabini	Cattle, sheep, wild ruminants	Eye, conjunctival sac, lacrimal duct	Muscid flies (*Musca* spp.)
Thelazia callipaeda	Dogs, cats, humans, primates, rabbits, foxes, bears, wolves, badgers	Eye, conjunctival sac, lacrimal duct	Muscid flies, fruit flies
Thelazia californiensis	Dogs, cats, sheep, deer, humans	Eye, conjunctival sac, lacrimal duct	Muscid flies
Thelazia lacrymalis	Horses, cattle	Eye, conjunctival sac, lacrimal duct	Face flies (*Musca* spp.)
Thelazia leesi	Camels	Conjunctival sac	Muscid flies

LIFE CYCLE 14. LIFE CYCLE OF *THELAZIA CALLIPAEDA*

Thelazia spp. are spirurid nematodes that infect the eye (1) of several mammals, including dogs, cats, rabbits, foxes, wolves and humans. The adult nematodes live under the eyelids and nictitating membrane of the hosts (1), and are sexually dimorphic. After mating, the females (viviparous) release large numbers of first-stage larvae (2) in the lacrimal secretions. The latter, free on the cornea, are ingested by sucking insects (*Phortica variegata*) that feed on eye secretions (3). *Phortica variegata* is active in Mediterranean regions between April and October when it actively seeks to feed on lacrimal secretions, thus acting as intermediate host of *T. callipaeda*. Within the insect, the L_1 remain encapsulated and develop to second- and third-stage larvae (4). The latter migrate from the coelomatic cavity of the intermediate host to the thorax and the buccal apparatus within 21 days. When the intermediate host feeds on a new susceptible host, the larvae are released from the proboscis and deposited onto the ocular mucosa (5), where they develop into sexually mature adults within four weeks, depending on the season. The other species of *Thelazia* are characterised by a similar life cycle, except for their intermediate hosts, belonging to flies of the family Muscidae.



Thelazia rhodesi

Description: Small, thin, yellowish-white worms 1–2 cm long. Males are 8–12 mm and females are 12–20 mm in length. A mouth capsule is present and the cuticle has prominent striations at the anterior end. The male worms have about 14 pairs of precloacal and three pairs of postcloacal papillae.

Life cycle: The prepatent period is 20–25 days.

Thelazia gulosa

Synonym: *Thelazia alfortensis*

Description: *Thelazia gulosa* are milky-white worms, with thin transverse cuticular striations (less evident in rear part of the body), and a large, deep, cup-shaped buccal cavity. Males are 4.8–10.9 mm long and have a variable number of precloacal papillae (from 8 to 33 pairs) and three pairs of postcloacal papillae. There are two asymmetrical spicules. The females are 4.8–18.8 mm long with a tapered caudal extremity.

Thelazia skrjabini

Description: Adult worms are whitish in colour, with transverse fine cuticular striations. The buccal cavity is small and shallow. Males are 5–11.5 mm long and curved posteriorly, with 16–32 pairs of precloacal and three pairs of postcloacal papillae. The spicules are unequal in length. The females are 7.5–21 mm long with a truncated caudal extremity.

Thelazia callipaeda

Description: Small thin white worms 1–1.7 cm long; males are 7–11.5 mm and females 7–17 mm in length. The cuticle bears fine transverse striations. The male has one single and five pairs of precloacal papillae and two pairs of postcloacal papillae. The left spicule is much longer (about 10 times) than the right. In the female, the vulva is in the oesophageal region. When laid, the eggs contain fully developed larvae.

Thelazia californiensis

Description: Small thin white worms 1–1.5 cm long. A mouth capsule is present and the cuticle has prominent striations at the anterior end. The male has 10 pairs of caudal papillae. The left spicule is long and slender and the right spicule short and stout.

Thelazia lacrymalis

Description: Small thin yellowish-white worms 1–2 cm long. Males are 8–12 mm and females 14–18 mm. A mouth capsule is present and the cuticle has prominent striations at the anterior end. In the male, the tail is blunt and recurved with caudal alae.

Life cycle: The prepatent period is about 3–6 weeks.

Oxyspirura

Eyeworms of birds found on the conjunctiva, under the nictitating membrane or in the nasal–lacrimal ducts.

Life cycle: The life cycle is indirect. Eggs pass through the lacrimal duct, are swallowed and shed in the faeces. These are ingested by an intermediate host and development to the infective stage occurs. Following consumption of the intermediate host by the definitive host, the larvae migrate from the oesophagus and pharynx to the eye via the lacrimal duct. The main species is *Oxyspirura mansoni* (syn. *Oxyspirura parvorum*) which infects the eye, conjunctiva and lacrimal ducts of chickens, turkeys and guinea fowl. This parasite has cockroaches and mayflies (Ephemeroptera) as intermediate hosts.

Oxyspirura mansoni

Synonym: *Oxyspirura parvorum*

Description: These are slender worms with a smooth cuticle and a globular-shaped pharynx; in the female, the vulva is near the tail. The males measure around 10–15 mm and the females 14–20 mm. The tail of the male is curved ventrally and alae are absent. Spicules are uneven, the right being short and stubby, the left long (about 15 times the length of the right spicule) and slender. In the female worm, the vulva is near the tail. The medium-sized ovoid egg is embryonated when laid and measures on average about 65 by 45 µm.

FAMILY GNATHOSTOMATIDAE

Gnathostoma

These are parasites of the stomach of carnivores (Table 1.36). The presence of the worms in gastric nodules is sufficient for generic diagnosis.

Gnathostoma spinigerum

Description: Thick-bodied worms, reddish at the front and greyish posteriorly. The males are 1–2.5 cm and the females up to 3 cm long. The presence of the worms in gastric nodules is sufficient for generic diagnosis. Confirmation is easily made with a hand lens when the swollen anterior head bulb covered with transverse rows of 6–11 small hooks will be seen. The head contains four submedian cavities that each communicate with a cervical sac. The anterior of the body is covered with flat cuticular spines and the ventral caudal region of the male bears small spines and four pairs of large

Table 1.36 *Gnathostoma* species.

Species	Hosts	Site	Intermediate hosts
Gnathostoma spinigerum	Cats, dogs, humans, mink, polecats and several wild carnivores	Stomach	Freshwater crustaceans, copepods
Gnathostoma hispidum	Pigs, rarely humans	Stomach	Freshwater crustaceans, *Cyclops* spp.
Gnathostoma doloresi	Pigs, wild boar	Stomach	Freshwater crustaceans

pedunculate papillae as well as several smaller sessile ones. The left spicule is longer than the right. The medium-sized eggs are oval, with a greenish shell which possesses fine granulations, and they have a thin cap at one pole. Eggs measure 69 by 37 µm and contain one cell or a morula when passed in faeces.

Life cycle: The adult worms live in tunnels in the gastric nodules, and the eggs pass from there into the lumen and are dropped into the water in the faeces where they hatch after several days. The crustaceans (first intermediate hosts) ingest L_1 and development to L_2 takes place. The crustaceans are themselves ingested by vertebrates (second intermediate hosts), such as fish, frogs and reptiles, and development to L_3 occurs and the larvae become encysted. The L_3 can also encyst in many mammals such as mice, rats and dogs. The final host is infected by ingestion of the vertebrate vector and further development occurs in the stomach wall, where the worms provoke the growth of fibrous lesions.

Gnathostoma hispidum

Description: Thick-bodied worms; the males are 1.5–2.5 cm and the females 2–4.5 cm long. Spiny scales cover the whole body of the worm. The left spicule is about three times longer than the right spicule. Eggs are oval, 72–74 by 39–42 µm, with a thin cap at one pole (Fig. 1.75).

Life cycle: The young worms migrate in the abdominal organs of the host, particularly the liver. Adult worms live in tunnels in the gastric nodules, and the eggs pass from there into the lumen and are dropped into the water in the faeces where they develop to L_2 before hatching after several days. Crustaceans ingest L_2 and development to L_3 takes place within about 10 days. The final host is infected by ingestion of the crustacean intermediate host and further development occurs in the stomach wall, where the deeply embedded worms provoke the growth of fibrous lesions. A second intermediate host is not required with *G. hispidum*.

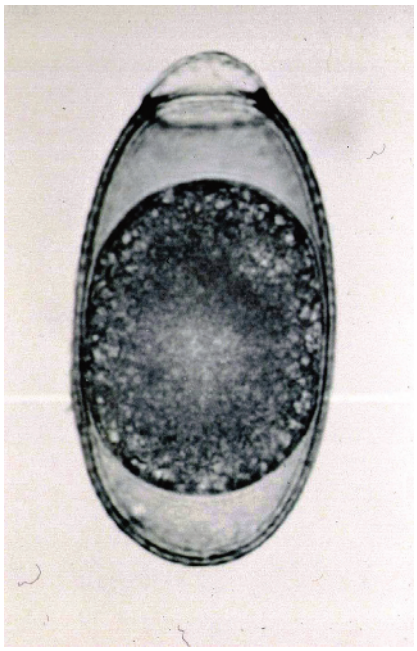


Fig. 1.75 *Gnathostoma hispidum* egg.

Gnathostoma doloresi

Description: Adult male worms are 2.6–2.8 cm long and female worms 3–4 cm long. The entire body surface has numerous transverse rows of backwardly directed cuticular spines. Anteriorly, the spines are broad and short, with several unequal teeth, becoming gradually smaller, with single-pointed spines posteriorly. The spicules are unequal, stout and curved, tapering evenly from root to tip.

Life cycle: As for *G. hispidum*.

FAMILY GONGYLONEMATIDAE

Gongylonema

Thread-like parasitic worms of mammals and birds often referred to as 'gullet worms', with over 30 species described (Table 1.37). Both sexes have cervical alae and the males possess caudal alae which are often asymmetrical.

Life cycle: The life cycle is typically spiruroid. Eggs are passed in faeces and when eaten by an intermediate host, they hatch and develop to the infective stage within about four weeks. Infection of the definitive host is through the ingestion of infected coprophagous beetles or cockroaches. The adult worms live spirally (in a zipper fashion) embedded in the mucosa or submucosa with their anterior and/or posterior ends protruding into the lumen. The prepatent period is about eight weeks.

Gongylonema ingluvicola

Description: These are long slender worms. The female worm is about 32–55 mm and the males around 18 mm long. The anterior end of the body has a number of longitudinal rows of round or oval, wart-like cuticular plaques. The eggs measure approximately 58 by 35 µm.

Table 1.37 *Gongylonema* species.

Species	Hosts	Site	Intermediate hosts
Gongylonema ingluvicola	Chickens, turkeys, partridges, pheasants, quails	Crop, oesophagus	Coprophagous beetles, cockroaches
Gongylonema monnigi	Sheep, goats	Rumen	Coprophagous beetles, cockroaches
Gongylonema pulchrum (syn. *Gongylonema scutatum*)	Sheep, goats, cattle, pigs, zebus, buffalo, horses, donkeys, deer, camels, humans, primates	Oesophagus, rumen	Coprophagous beetles, cockroaches
Gongylonema verrucosum	Cattle, sheep, goats, deer, zebus	Rumen, reticulum, omasum	Coprophagous beetles, cockroaches
Gongylonema macrogubernaculum	Old and New World Monkeys	Oesophagus, tongue, buccal cavity	Coprophagous beetles, cockroaches

Gongylonema monnigi

Description: A long, slender, whitish worm, the males being about 4 cm and the females up to about 11 cm in length. Similar to *G. verrucosum* except the cervical ala is not festooned and the shape of the gubernaculum differs.

Gongylonema pulchrum

Synonym: *Gongylonema scutatum*

Description: A long, slender, whitish worm, the males being about 5 cm and the females up to about 14 cm in length. Worms are easily distinguished microscopically by the presence of longitudinal rows of cuticular bosses in the anterior region of the body. Asymmetrical cervical alae are prominent. The tail of the male has asymmetrical alae with 10 pairs of papillae. The left spicule is long and slender whereas the right spicule is short and stout. The male has a gubernaculum. The egg is thick-shelled and possesses two opercula. It measures 50–70 by 25–37 µm and contains an L_1 when passed in faeces.

Gongylonema verrucosum

Description: Long slender worms, reddish when fresh. The males are about 3.5 cm and the females 7–9.5 cm in length. The adult worms have a festooned cervical ala and cuticular bosses only on the left side of the body. The males' spicules are unequal in length with the left spicule considerably longer than the right.

Gongylonema macrogubernaculum

Description: These are long thin whitish worms, the males measuring about 5 cm and the females around 14 cm in length. Worms are characterised by the presence of longitudinal rows of cuticular bosses in the anterior region of the body.

FAMILY SPIRURIDAE

Nematodes of the family Spiruridae are found in the upper digestive tract of mammals and birds (Table 1.38).

Spirura/Odontospirura

Life cycle: The life cycle is typically spiruroid. Eggs develop into infective larvae within an intermediate host. Larvae may be ingested by paratenic hosts, such as rodents and lizards, in which they become encapsulated. The final host becomes infected by ingesting the insects or their transport hosts.

Table 1.38 *Spirura* species.

Species	Hosts	Site	Intermediate hosts
Spirura ritypleurites	Cats, rarely dogs, foxes	Stomach	Beetles, cockroaches
Spirura uncinipenis (syn. *Sicarius uncinipenis*)	Rheas	Proventriculus	Beetles, cockroaches
Spirura zschokkei (syn. *Vaznema zschokkei*)	Rheas	Proventriculus	Beetles, cockroaches
Odontospirura cetiopenis	Rheas	Proventriculus, gizzard	Beetles, cockroaches

Spirura ritypleurites

Description: Thick, short, white worms with the posterior region thicker than the anterior and twisted in a spiral. Male worms measure up to 26 mm and females can be 30 mm in length. The anterior area of the cuticle is inflated on the underside and the transverse striations are prominent. The eggs have a thick shell and are embryonated when passed and measure up to 52 by 36 µm.

Spirura uncinipenis

Synonym: *Sicarius uncinipenis*

Description: Males measure 15–20 mm and females 16–26 mm. The spicules are short and unequal in length.

Spirura zschokkei

Synonym: *Vaznema zschokkei*

Description: Male worms measure 16–17 mm and females 17–25 mm in length. The spicules are long and filiform.

Odontospirura cetiopenis

Description: The body is spirally coiled, with male worms measuring 15–17 mm and females 20–23 mm. Four pairs of cephalic papillae are present at the base of the lips. Males have caudal alae and long spicules of equal length.

FAMILY TETRAMERIDAE

Tetrameres

Parasites of this genus show sexual dimorphism. The male worms are pale white, small and slender and lie in the lumen of the proventriculus of birds (Table 1.39). The females are bright red and almost spherical, and lie embedded in the proventricular glands. Cordons are absent.

Life cycle: Eggs are shed with the faeces and hatch when eaten by an intermediate host. The final host becomes infected following ingestion of the intermediate host and the males and females locate in the glands of the proventriculus. Males inhabit the mucosal surface and upper regions of the glands but after mating they leave the glands and die. The females are embedded deep in the mucosal glands.

Tetrameres americana

Synonym: *Tropisurus americana*

Description: The adults show sexual dimorphism. The males are pale, white, slender and only about 5–6 mm long. The females are bright red and almost spherical, with a diameter of about

Table 1.39 *Tetrameres* species.

Species	Hosts	Site	Intermediate hosts
Tetrameres americana (syn. *Tropisurus americana*)	Chickens, turkeys, ducks, geese, grouse, quails, pigeons	Proventriculus	Cockroaches, grasshoppers, beetles
Tetrameres fissispina (syn. *Tropisurus fissispina*)	Ducks, geese, chickens, turkeys, pigeons and wild aquatic birds	Proventriculus	Crustaceans (*Daphnia* and *Gammarus*), grasshoppers, earthworms
Tetrameres crami	Domestic and wild ducks	Proventriculus	Crustaceans (*Gammarus* and *Hyalella*)
Tetrameres confusa	Chickens	Proventriculus	?
Tetrameres mohtedai	Chickens	Proventriculus	?
Tetrameres pattersoni	Quails	Proventriculus	?

3.5–4.5 mm (Fig. 1.76). Males have spiny cuticles and no cordons; females have four longitudinal deep furrows on the surface. Eggs are oval, thick-shelled, 42–60 by 24–45 µm and embryonated when passed. They are transparent in appearance and have thickened poles (see Fig. 4.8).

Tetrameres fissispina

Synonym: *Tropisurus fissispina*

Description: See *T. americana*. Males are pale, white, slender and 5–6 mm long. The females are bright red, ovoid/spherical, with a diameter varying from around 2.5 to 6 mm. Males have four longitudinal rows of spines along the median and lateral lines and no cordons; females have four longitudinal deep furrows on the surface. Eggs are essentially similar to those of *T. americana* and measure 48–56 by 26–30 µm.

Tetrameres crami

Description: Males are white, slender and about 4 mm long. The red ovoid/spherical females measure around 2 mm by 1.5 mm.

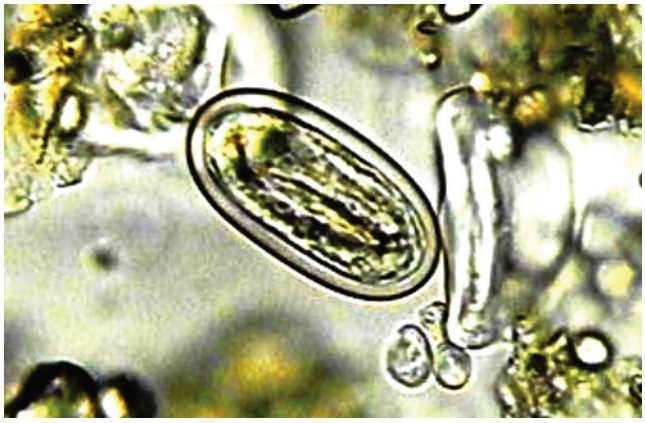


Fig. 1.76 Adult female *Tetrameres americana*.

FAMILY HARTERTIIDAE

Hartertia

The main species is *Hartertia gallinarum* which infects the small intestine of chickens and bustards. This parasite has termites as intermediate hosts.

Hartertia gallinarum

Description: Slender worms and exceptionally long for a spiruroid. The males measure up to around 40 mm and the females up to 110 mm in length. The gross appearance of the worms closely resembles that of *Ascaridia galli* and they have two lateral lips, each divided medially into three lobes. The posterior of the male has lateral alae, ventral cuticular bosses and four pairs of precloacal and two pairs of postcloacal papillae. The left spicule has a barbed expansion at its tip and is about four times larger than the blunt-ended right spicule. Eggs are thick-shelled, 45–53 by 27–33 µm, and are embryonated when passed.

Life cycle: Eggs are passed in faeces and, when ingested by a termite, develop to the infective stage in the body cavity. Following ingestion of an infected intermediate host, the larvae develop to maturity in the final host in about three weeks.

FAMILY PNEUMOSPIRIDAE

Members of this family are lungworms of wild felids and include species within the genera *Metathelazia* and *Vogeloides*.

SUPERFAMILY PHYSALOPTEROIDEA

FAMILY PHYSALOPTERIDAE

Physaloptera

The genus *Physaloptera* includes a number of species that are parasites of the stomach of mammals and other vertebrates. In particular, *Physaloptera praeputialis* infects cats, wild felids and rarely dogs, whereas *Physaloptera rara* infects cats and dogs.

Life cycle: The life cycle is typically spiruroid. Eggs passed in the faeces of the infected host develop into infective larvae if ingested by coprophagous beetles, crickets and other insects. The life cycle is completed when cats ingest the intermediate hosts. Various cold-blooded transport hosts may also be involved in transmission of infection. The prepatent period is around 8–10 weeks.

Physaloptera praeputialis

Description: Adult worms are white or pinkish in colour and larger than most spiruroids, being stout and resembling ascarids. Males measure 1–45 mm and females 2–60 mm. The cuticle in both sexes extends posteriorly as a sheath (pseudolabia) beyond the end of the body and the mouth is surrounded by a cuticular collar. The lips are simple and bear a set of three flattened internal teeth and a single conical external tooth. The male bears lateral alae, joined anteriorly

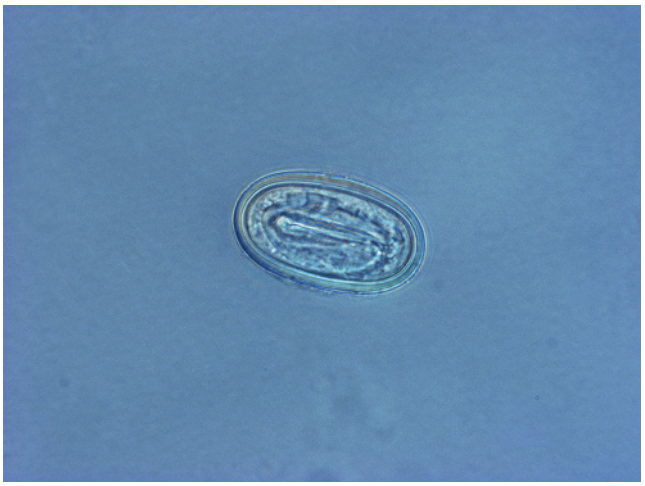


Fig. 1.77 *Physaloptera* egg. (Courtesy of Jana Bulantová).

across the ventral surface. In the female, the vulva is slightly anterior to the mid-body. The larvated eggs have a thick clear shell and measure 45–58 by 30–36 µm (Fig. 1.77).

Physaloptera rara

Description: Adult male worms are 2.5–3 cm and females 3–6 cm long. This species differs from *P. praeputialis* in that there is no sheath over the posterior portion of the body in both sexes. The female vulva is anterior to the middle of the body. Eggs are thick-shelled and ellipsoid, 42–53 by 29–35 µm.

SUPERFAMILY DRACUNCULOIDEA

Members of this superfamily are parasites of the subcutaneous tissues. The two genera of veterinary significance are *Dracunculus* and *Avioserpens*. The life cycle involves development in a species of *Cyclops* before becoming infective to the final host.

FAMILY DRACUNCULIDAE

Dracunculus

This genus includes the 'guinea worm', an important parasite affecting humans, and the North American guinea worm found in carnivores. The male worms are very much smaller than the females and the latter are one of the longest of the common nematodes in human and animals.

Life cycle: This is indirect. Adult worms mature in deep connective tissue and then migrate to peripheral subcutaneous tissue about nine months after initial infection. A cutaneous blister develops around the head end of the worm and when this makes contact with water, the uterus of the worm ruptures and liberates large numbers of L_1 larvae. Release of larvae can continue over several weeks if the lesion is repeatedly immersed in water. These larvae develop to the infective stage in a species of *Cyclops*. Infection of the final host is through ingestion of infected copepods with drinking water or within paratenic hosts.

Dracunculus medinensis

Description: Males measure about 2–3 cm; females are much larger, being around 100 cm long and 1.5–2 mm in width, but they can reach up to 300 cm in length. The anterior of the worms possess a 'helmet'. Females have no vulva.

Life cycle: Infection is caused by drinking water containing copepods, which are infected with larvae of *D. medinensis*. Following ingestion by the hosts (e.g. human; occasionally cattle, horse, dog, cat and other mammals), the copepods die and release the larvae, which penetrate the host stomach and intestinal wall and enter the abdominal cavity. After maturation into adults and copulation, the male worms die and the females migrate in the subcutaneous tissues near the skin surface, where the female worm induces a blister on the skin that ruptures. When this lesion comes into contact with water, the female worm emerges and releases larvae, which if ingested by a copepod develop into infective larvae after about two weeks. The prepatent period is around 12 months.

Dracunculus insignis

Description: Adults are white cylindrical worms 17.6–23 cm in length and 3–4 mm at maximum width. The females are much larger than the males and are filled with first-stage larvae. This species can be differentiated from *D. medinensis* by the number of preanal papillae and also the length of the gubernaculum.

Life cycle: Similar to *D. medinensis*. Development in the copepod is around three weeks. Hosts are mink, raccoon, otter, wild carnivores; occasionally dog and cat. Frogs can also act as paratenic intermediate hosts.

Avioserpens

Avioserpens are parasites of ducks and are found in subcutaneous swellings.

Life cycle: Larvae are released into water and infective stages have been shown to occur in *Cyclops*. Infection of the final host occurs through ingestion of the intermediate host.

Avioserpens taiwana

Synonyms: *Filaria taiwana*, *Oshimaia taiwana*, *Avioserpens denticulophasma*, *Petroviprocta vigissi*

Description: The female measures up to about 25 cm in length by 0.8 mm in width. The anterior end is blunt and a chitinous rim, carrying two prominent lateral papillae, surrounds the mouth. Four smaller papillae are found further back on the head. The large uterus contains larvae. The anus, vagina and vulva are atrophied. A conical papilla is sited at the termination of the tail. The male worm is unknown.

SUPERFAMILY ACUARIOIDEA

Members of the Acuarioidea (formerly Spiruroidea) are small to medium-sized nematodes inhabiting the upper alimentary tract of birds. The species are characterised by the presence of peculiar cuticular cephalic structures (cordons) extending posteriorly, and sometimes recur forwards.

FAMILY ACURIDAE

Echinuria

The main species is *Echinuria uncinata* (syn. *Acuaria uncinata*) which infects the oesophagus, proventriculusand gizzard of ducks, geese, swans and various aquatic birds. This parasite has *Daphnia* and *Gammarus* as intermediate hosts.

Echinuria uncinata

Synonym: *Acuaria uncinata*

Description: These are small whitish worms with a slender body. Males measure 8–10 mm and females 12–18.5 mm long. The cuticle is ornamented with four wavy cordons that are non-recurrent and they anastomose in pairs and do not extend beyond the oesophagus section. Four rows of longitudinal spines are present on the cuticle. In the male, there are four pairs of precloacal papillae in two groups of two either side, and four pairs of postcloacal papillae. The left spicule is about 3–4 times longer than the right spicule. The small ellipsoidal eggs are thick-shelled with a smooth surface. They measure on average 37 by 20 µm and are embryonated when passed (see Fig. 4.8).

Life cycle: Eggs are passed in the faeces and ingested by water fleas in which they hatch and develop to infective larvae. The parasites continue development when the intermediate host is ingested by an aquatic bird.

Dispharynx

The main species is *Dispharynx nasuta* (syn. *Dispharynx spiralis*, *Acuaria spiralis*, *Acuaria nasuta*) which infects the oesophagus and proventriculus of chickens, turkeys, pigeons, guinea fowl, grouses pheasants and other birds. This parasite has isopods, including sowbugs (*Porcellio*) and pillbugs (*Armadillidium*), as intermediate hosts.

Dispharynx nasuta

Synonyms: *Dispharynx spiralis*, *Acuaria spiralis*, *Acuaria nasuta*

Description: The body is slender and coiled, particularly the posterior of the male. Males measure up to around 8 mm and the females 10–12 mm long. The cuticle is ornamented with four wavy cordons that recurve anteriorly and do not fuse. The male has four pairs of precloacal and five pairs of postcloacal papillae. The left spicule is slender and the right spicule shorter and oval-shaped. The eggs are thick-shelled, 33–40 by 18–25 µm, and embryonated when passed.

Life cycle: The intermediate host ingests embryonated eggs and development to L_3 takes place in the body cavity. When the isopod is consumed by the final host, the worms develop to the final stage in the proventriculus or oesophagus.

Cheilospirura

The main species is *Cheilospirura hamulosa* (syn. *Acuaria hamulosa*) which infects the gizzard of chickens and turkeys. This parasite has grasshoppers (*Melanoplus*), weevils and beetles as intermediate hosts.

Cheilospirura hamulosa

Synonym: *Acuaria hamulosa*

Description: The worms have four, double-wavy, irregular, cuticular ridged cordons that extend to more than half the length of the body. These cordons do not anastomose or recur anteriorly. Male worms measure up to 15 mm and females 30 mm. The males have four pairs of precloacal and six pairs of postcloacal papillae, a short flattened spicule on the right and a longer slender spicule on the left side. The oval eggs measure about 40–45 by 24–47 µm and are embryonated when passed. The egg is very similar in size and appearance to that of *Dispharynx*.

Life cycle: Eggs shed in the faeces are ingested by the intermediate host where they develop to the infective stage in about three weeks. The final host becomes infected after consuming this intermediate host and the prepatent period is about three weeks.

Streptocara

These worms are of minor importance in domestic livestock. The main species is *Streptocara crassicauda* which infects the gizzard of ducks and chickens. This parasite has crustacea (*Gammarus*) as intermediate hosts.

Streptocara crassicauda

Description: Males are about 5 mm and females up to 10 mm in length. The cervical alae are well developed and possess small teeth on the posterior margin.

Life cycle: Little is known of the life cycle.

SUPERFAMILY FILARIOIDEA

This superfamily is closely related to the Spiruroidea and, as in the latter, all its genera have indirect life cycles. None of them inhabits the alimentary tract, and they depend on insect vectors for transmission.

Within the superfamily, differences in biological behaviour are seen, the more primitive forms laying eggs, which are available to the vectors in dermal exudates, and the more highly evolved forms laying larvae, termed microfilariae. The latter, which may be enclosed in a flexible sheath-like 'eggshell', are taken up by parasitic insects feeding on blood and tissue fluids. In some species, the microfilariae only appear in the peripheral blood and tissues at regular intervals, some appearing in the daytime and others at night; this behaviour is termed diurnal or nocturnal periodicity.

Genera of interest in veterinary medicine include the Filariidae: *Parafilaria*, *Stephanofilaria*, *Suifilaria*; and the Onchocercidae: *Onchocerca*, *Dirofilaria*, *Acanthocheilonema*, *Pelecitus*, *Chandlerella*, *Setaria*, *Elaeophora*, *Splendidofilaria* and *Paronchocerca*.

FAMILY FILARIIDAE

Parafilaria

Adults of this genus of primitive filarioids live under the skin of cattle and buffalo (i.e. *Parafilaria bovicola*), horse, donkey and other equids (*Parafilaria multipapillosa*), where they produce inflammatory lesions or nodules.

Parafilaria bovicola

Description: Small slender white worms about 3–6 cm in length. Males are 2–3 cm and females 4–6 cm long. Anteriorly, there are numerous papillae and circular ridges in the cuticle. The rest of the cuticle is striated transversely. In the female, the vulva is situated anteriorly near the simple mouth opening and the tail is blunt with no papillae. The tail of the male is blunt and short. The caudal alae are supported by precloacal and postcloacal papillae. Small embryonated eggs, 45 by 30 µm, that have a thin flexible shell are laid on the skin surface where they hatch to release the microfilariae or L_1, which are about 200 µm in length.

Life cycle: Eggs or free L_1 present in exudates from bleeding points in the skin surface are ingested by muscid flies (e.g. *Musca autumnalis* in Europe, *M. lusoria* and *M. xanthomelas* in Africa) in which they develop to L_3 within several weeks to months, depending on air temperature. Transmission occurs when infected flies feed on lacrimal secretions or skin wounds in other cattle and the L_3 deposited then migrate in the subcutaneous tissue and develop to the adult stage under the skin in 5–7 months. Bleeding points develop 7–9 months after infection, which is about the same duration as patency.

Parafilaria multipapillosa

Synonym: *Filaria haemorrhagica*

Description: Slender white worms 3–7 cm in length. Adult males are 28 mm and females 40–70 mm in length. The anterior end of the worm bears a large number of papilliform thickenings. The small embryonated eggs (around 55 × 30 µm) have a thin flexible shell and are laid on the skin surface where they hatch to release the microfilariae or L_1; these are about 200 µm in length and have a rounded posterior extremity.

Life cycle: Eggs or free L_1 larvae present in exudates from bleeding points in the skin surface are ingested by horn flies (*Haematobia*), in which they develop to L_3 within several weeks to months, depending on air temperature. Transmission occurs when infected flies feed on lacrimal secretions or skin wounds in other horses and the L_3 deposited then migrate in the subcutaneous tissue and develop to the adult stage under the skin in 9–12 months.

Stephanofilaria

Worms of this genus inhabit the dermis and cause chronic dermatitis in cattle, buffalo, rhinoceros and elephants in the tropics and subtropics (Table 1.40). The genus is readily recognised because the worms are small, and the oral opening is surrounded by numerous spines.

Life cycle: The fly vectors are attracted to the open lesions in the skin caused by the adult parasites, and ingest the microfilariae in the exudate. Development to L_3 takes about three weeks, and the final host is infected when the flies deposit larvae on normal skin.

Stephanofilaria dedoesi

Description: Small nematodes; males are 2.3–3.2 mm and females 6.1–8.5 mm in length. A protruding cuticular rim, with a denticulate edge, surrounds the oral aperture. The anterior of the worms has a circular thickening, which possesses a number of small cuticular spines. An anus is absent in female worms. The male spicules are of unequal length.

Table 1.40 *Stephanofilaria* species.

Species	Hosts	Site	Intermediate hosts
Stephanofilaria assamensis	Cattle, goats, buffalo	Skin, back	Muscid flies
Stephanofilaria kaeli	Cattle	Skin, head, legs, teats	Muscid flies
Stephanofilaria dedoesi	Cattle	Skin, head, legs, teats	Muscid flies
Stephanofilaria okinawaensis	Cattle	Skin, face and teats	Muscid flies
Stephanofilaria stilesi	Cattle	Skin, lower abdomen	Horn flies (*Haematobia* spp.)
Stephanofilaria zaheeri	Buffalo, cattle	Skin, ears, legs, teats	Muscid flies

Stephanofilaria stilesi

Description: Small nematodes; males are 2.6–3.7 mm and females 3.7–6.9 mm in length. There are 4–5 cephalic spines and 18–19 peribuccal spines. The male spicules are unequal and the female worms have no anus. The thin-shelled eggs are 58–72 by 42–55 µm in size. Microfilariae are 45–60 µm in length and are characterised by a peribuccal elevation with a single spine and a short and rounded tail.

Stephanofilaria okinawaensis

Description: The parasites are small, rounded, whitish and slender bodied. Females are 7–8.5 mm and males 2.7–3.5 mm in length.

Suifilaria

These worms can be associated with dermal abscesses but are generally of little veterinary significance.

Life cycle: Not known. The females appear to lay their eggs in the skin of the pig. The main species is *Suifilaria suis* which infects the subcutaneous connective tissue of pigs. The intermediate host is not known.

Suifilaria suis

Description: These are slender worms. Male are 17–25 mm and females 34–40 mm in length. The male only has one caudal ala and this is on the left. The hind end of the male is spirally coiled and the spicules are unequal, with the left shorter than the right. The tail of the female bears a number of small tubercles on its tip, which ends abruptly. Small embryonated eggs, 51–61 by 28–32 µm, have a thin flexible shell and are laid on the skin surface where they hatch to release the microfilariae or L_1, which are about 200 µm in length.

FAMILY ONCHOCERCIDAE

Dirofilaria

Of the two species occurring in domestic carnivores, *Dirofilaria immitis* is by far the more important since adults are found in the right side of the heart and adjacent blood vessels of dogs, being

responsible for canine heartworm disease. Adults of *Dirofilaria repens* are localised in the subcutaneous tissues. Both species infect dog, fox, wild canids, occasionally cat and rarely human and primates.

Dirofilaria immitis

Description: Long slender white/grey worms measuring 15–30 cm in length with a tough cuticle. Adult females measure 25–30 cm, with the males about half as long. Many worms are usually found together in a tangled mass. The size and site are diagnostic for *D. immitis*. The male tail has the typical loose spiral common to the filarioids (Fig. 1.78), and the tail bears small lateral alae. There are 4–6 pairs of ovoid papillae. The left spicule is long and pointed; the right spicule is smaller and ends bluntly. In the female, the vulva is situated just behind the end of the oesophagus. The microfilariae in the blood are not ensheathed and are 307–332 µm in length by 6.8 µm wide. They have a tapered anterior end and blunt posterior end.

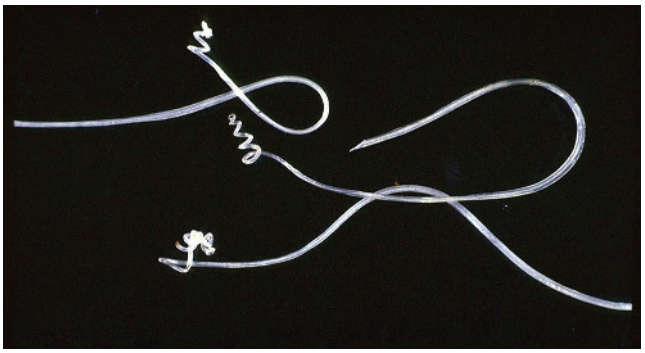
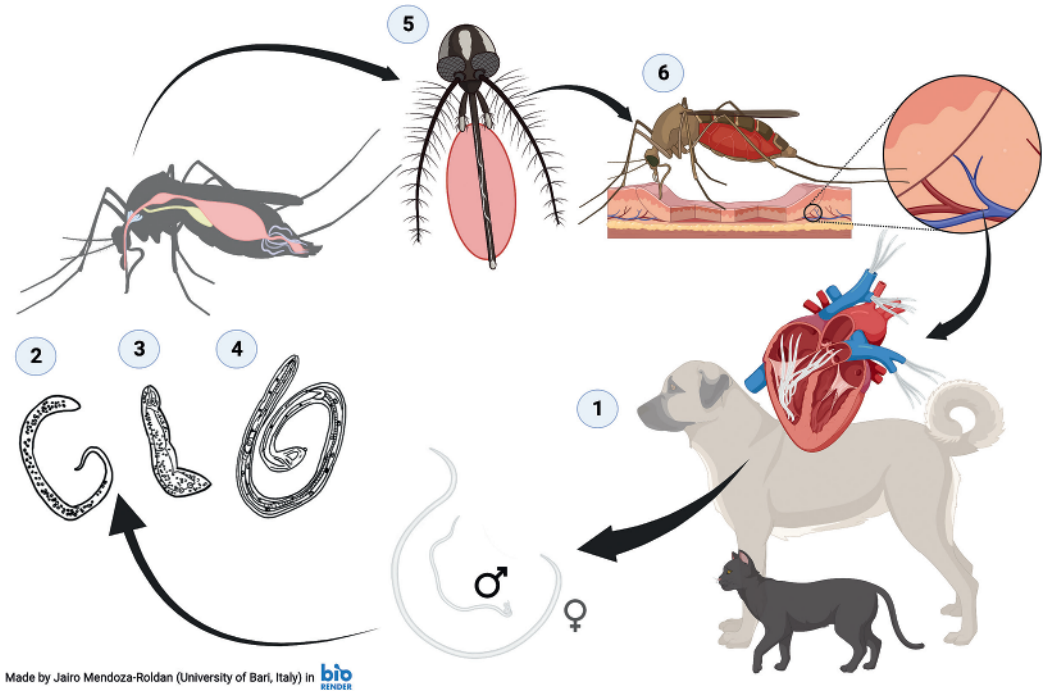


Fig. 1.78 Adult *Dirofilaria immitis* heartworms.

Life cycle: The adults live in the heart and adjacent blood vessels and the females release microfilariae directly into the bloodstream. These microfilariae can live for several months in the visceral blood vessels. Microfilariae are ingested by female mosquitoes during feeding. Development to infective L_3 in the malpighian tubules of the mosquito takes about two weeks. The infective L_3 then migrate to the mouthparts and the final host is infected when the mosquito takes a further blood meal. In the dog, the L_3 migrate to the subcutaneous or subserosal tissues in the thorax or abdomen and undergo two moults over the next few months; only after the final moult do the young *D. immitis* pass to the heart via the venous circulation. The minimum prepatent period is about six months. The adult worms survive for several years and patency has been recorded for over five years. See **life cycle 15**.

LIFE CYCLE 15. LIFE CYCLE OF *DIROFILARIA IMMITIS*

Adults of *Dirofilaria immitis* live in the right side of the heart, and in the pulmonary artery and its branches of dogs and cats, that act as definitive hosts (1). After mating, the females release first-stage larvae (microfilariae, 2) directly into the circulatory system. When intermediate hosts (mosquitoes of the genera *Culex*, *Aedes* and *Anopheles*) feed on an infected host, they ingest the microfilariae; these pass through the midgut into the haemocoel and eventually, in the malpighian tubules, they moult within 2–4 weeks to second-stage larvae ('sausage-like', 3) and subsequently to infective third-stage larvae (long and thin) (4). The larvae then migrate to the labium of the mosquito mouthparts (5); from here, they can be inoculated into the circulation of a susceptible host during the insect's next blood meal (6). The larvae then begin migrating toward the final site of infection; the first preadult forms in the pulmonary artery and right ventricle at 70–85 days post infection and reaches sexual maturity at 120 days post infection (1). Microfilariae start to be produced 6–9 months post infection and can be detected in blood vessels.



Dirofilaria repens

Synonym: *Nochtiella repens*

Description: The adults are long slender worms measuring from around 5 cm up to 17 cm in length. Males are 5–7 cm and females 13–17 cm. Microfilariae measure 360 by 12 µm.

Life cycle: The adults live in subcutaneous nodules and the females release microfilariae, which migrate to the blood and are ingested by female mosquitoes during feeding. Development to L_3 takes place in the mosquito and the final host is infected when the mosquito takes a further blood meal. In the dog, the L_3 migrate to the subcutaneous or subserosal tissues and undergo two moults over the next few months. The prepatent period is 27–34 weeks.

Acanthocheilonema

Several species of *Acanthocheilonema* (formerly *Dipetalonema*), transmitted mainly by fleas, lice and mosquitoes, occur in the subcutis of dogs and various canids in tropical and subtropical zones. While *A. reconditum* is mainly present in the subcutaneous tissues, *A. dracunculoides* is found in the peritoneum and kidney, being transmitted by louse flies.

Acanthocheilonema reconditum

Synonym: *Dipetalonema reconditum*

Description: The slender male worms measure on average 1.5 cm and females about 2.5 cm. The male spicules are unequal. The unsheathed microfilariae are less than 300 µm in length and have a blunt head and hooked posterior end with button-hook tails.

Life cycle: Following ingestion of a blood meal, the microfilariae develop to the infective third stage in about 7–14 days and then migrate to the head. Larvae pass to the host when the intermediate host next feeds. The prepatent period in the dog is 8–10 weeks. *Acanthocheilonema reconditum* shows a diurnal periodicity.

Acanthocheilonema dracunculoides

Synonym: *Dipetalonema dracunculoides*

Description: The adult worms are small; male worms are 2.4–3 cm, females 3.2–6 cm in length. Males have broad unequal spicules.

Cercopithifilaria

Cercopithifilaria bainae

Description: Skin microfilariae are unsheathed and the cephalic end is rounded with a slight protuberance bearing a tiny cephalic hook. The body is short (mean length of 183.1 ± 7.8), flattened dorsoventrally and constant along its length, except for the posterior conical end (Fig. 1.79). The body cuticle is thick bearing transverse striations.

Life cycle: The life cycle occurs in *Rhipicephalus sanguineus* sensu lato in which microfilariae develop to infective larvae in about four weeks under experimental conditions. Larvae pass to dogs when the intermediate host next feeds on another individual.

Fig. 1.79 Microfilaria of *Cercopithifilaria bainae*.

Cercopithifilaria grassii

Synonym: *Dipetalonema grassii*, *Acanthocheilonema grassii*

Description: The adult worms are small, the females measuring about 2.5 cm in length. Microfilariae are large, up to 800 µm in length, with a hook-shaped tail.

Life cycle: The life cycle has not been described in detail. Following ingestion of a blood meal, the microfilariae develop to infective larvae in the intermediate hosts, which are ticks. Larvae pass to the host when the intermediate host next feeds off blood on a dog.

Dipetalonema

Several species of *Dipetalonema*, transmitted mainly by mosquitoes, occur in the subcutis, peritoneum, pleura or blood vessels of mammals in tropical and subtropical zones. The main species is *Dipetalonema evansi* (syn. *Deraiophoronema evansi*) which infects the heart, arteries and veins, pulmonary arteries, spermatic arteries and lymph nodes of camels. This parasite has mosquitoes of the genus *Aedes* as intermediate hosts.

Dipetalonema evansi

Synonym: *Deraiophoronema evansi*

Description: These are fairly large filarial worms; adult male worms are 8–11 cm, adult females 14.5–18.5 cm. Microfilariae are ensheathed, 200–315 µm in length and found in the peripheral blood.

Life cycle: The life cycle has not been described in detail but *Aedes* mosquitoes are thought to act as intermediate hosts. Following ingestion of a blood meal, the microfilariae develop to infective larvae in the intermediate host. Larvae pass to the host when the intermediate host next feeds.

Onchocerca

Though onchocercosis is an important filarial infection in human medicine (*Onchocerca volvulus* causing river blindness), most species in domestic animals are relatively harmless (Table 1.41).

Table 1.41 *Onchocerca* species.

Species	Hosts	Site	Intermediate hosts
Onchocerca gutturosa (syn. *Onchocerca lienalis*)	Cattle, camels	Connective tissue, ligamentum nuchae, gastrosplenic ligament	Blackflies (*Simulium*)
Onchocerca gibsoni	Cattle	Connective tissue	Midges (*Culicoides*)
Onchocerca ochengi (syn. *Onchocerca dermata*)	Cattle	Connective tissue, scrotum and udder	Unknown
Onchocerca armillata	Cattle, buffalo, sheep, goats, occasionally camels	Thoracic aorta	Midges (*Culicoides*), blackflies (*Simulium*)
Onchocerca dukei	Cattle	Abdomen, thorax, thighs	Unknown but probably blackflies
Onchocerca cebei (syn. *Onchocerca sweetae*)	Buffalo	Abdomen, thorax, thighs	Midges (*Culicoides*)
Onchocerca cervicalis	Horses	Cervical ligament	Midges (*Culicoides*)
Onchocerca fasciata	Camels	Connective tissue, ligamentum nuchae	Unknown
Onchocerca lupi	Dogs, cats, humans, wolves	Eyeball, conjunctiva, sclera, spinal channel	Unknown
Onchocerca tarsicola	Deer	Legs	Blackflies (*Simulium*)
Onchocerca reticulata	Horses, donkeys	Connective tissue, flexor tendons	Midges (*Culicoides*)
Onchocerca volvulus	Humans	Dermis, eye	Blackflies (*Simulium*)

Life cycle: The life cycle of *Onchocerca* is typically filarioid, with the exception that the microfilariae occur in the tissue spaces of the skin rather than in the peripheral bloodstream. Microfilariae migrate in subdermal connective tissue in the skin of the back, sometimes ears and neck, where biting flies, feeding in this area, ingest microfilariae, which then develop to the infective stage in around three weeks. When these infected insects feed on another animal, host transmission of L_3 occurs.

Onchocerca gutturosa

Synonym: *Onchocerca lienalis*

Description: Slender whitish worms; males range from 2 to 6 cm, while females are up to 60 cm in length or longer and are coiled in fibrous tissues. The cuticle possesses spiral thickenings to aid attachment. Microfilariae are 250–265 µm long and unsheathed.

Onchocerca gibsoni

Description: The slender worms range from 2 cm to over 20 cm in length and lie tightly coiled in tissue nodules. Males are 3–5 cm and females 14–20 cm although there have been reports of worms up to 50 cm in length. The tail of the male is ventrally curved and bears lateral alae and 6–9 papillae at either side. The spicules are unequal in size. Microfilariae are not sheathed and are 240–280 µm long and found mainly in the brisket area. The cuticle possesses transverse striations.

Onchocerca lupi

After its first description in a Caucasian wolf from Georgia, *Onchocerca lupi* remained almost unknown for decades until being reported in dogs from southern Europe (Greece, Portugal) and Germany, Israel, Hungary, Romania and Switzerland, and cats from the south of Iran, Portugal and Romania. In the western United States, cases of canine and feline onchocercosis are also reported. Since 2011, when the first report of human ocular infestation was described in Turkey, other human cases of *O. lupi* have been identified in patients from Germany, Turkey, Tunisia, Iran and the US.

Description: Adults of *O. lupi* are white and slender with rounded anterior ends and a multilayer tick cuticle with characteristic annular ridges 2–3 µm high and wide and evenly spaced at 25–30 µm intervals. Males are 4.3–5 cm long with two unequal spicules and the females longer (up to 16.5 cm) containing two uteri. However, their exact length is currently unknown due to the difficulty in removing complete adult females from the subcutaneous nodules where males and females copulate. The females develop microfilariae inside their uteri, which are released to subcutaneous tissues. Microfilariae are unsheathed, straight (81–115 µm in length) and have a bluntly rounded anterior end and a bent tail posterior end (Fig. 1.80).

Life cycle: The life cycle of *O. lupi* involves canids as definitive hosts and unknown arthropod species as intermediate hosts. Many aspects of the biology and ecology of *O. lupi* remain unknown. In the definitive hosts, male and female adult stages usually develop in the connective tissue of the subconjunctiva, conjunctiva, eyelids and nictitating membrane sitting on top of the sclera until reaching sexual maturity. Aberrant migration to the laryngeal soft tissue in dogs and spinal cord in humans has also been reported. The lifespan of adult worms in dogs has been estimated to be 3–8 years.

Onchocerca armillata

Description: Slender whitish worms. Male worms are about 7 cm and female worms up to 70 cm long. Microfilariae are unsheathed and measure 346–382 µm.

Fig. 1.80 Microfilaria of *Onchocerca lupi*.

Onchocerca cervicalis

Description: The male is 6–7 cm in length and the female up to 30 cm long.

Onchocerca reticulata

Description: Slender whitish worms; males are 15–20 cm and females over 50 cm long. Microfilariae are 330–370 µm and possess a long whiplash tail.

Life cycle: The prepatent period is around 12–16 months.

Pelecitus

The members of this genus are filarioid worms of birds and mammals (Table 1.42).

Pelecitus clavus

Synonym: *Eulimdana clava*

Description: Small to medium-sized worms which have helical turns. Male worms are 6–7 mm and female worms 17–20 mm long. The male spicules are unequal in length, the left being larger than the right.

Life cycle: Microfilariae are present in the blood or subcutaneous space of infected birds and are ingested by biting ectoparasite vectors when they feed.

Pelecitus scapiceps

Synonyms: *Dirofilaria scapiceps*, *Loaina scapiceps*

Description: Male worms are 11–16 mm in length with spicules of unequal length. Female worms are 25–30 mm long.

Life cycle: Microfilariae circulate in the blood of infected lagomorph hosts (there is no circadian periodicity). Microfilariae ingested by a mosquito develop into infective third-stage larvae and these are then injected into the definitive host during feeding. These larvae migrate in the subcutaneous tissue to a maturation site, such as the main body, and develop to the early fifth stage before migrating to the hocks where they develop into mature adult worms. The prepatent period can vary around 130–220 days.

Table 1.42 *Pelecitus* species.

Species	Hosts	Site	Intermediate hosts
Pelecitus clavus (syn. *Eulimdana clava*)	Pigeons, wild birds and occasionally humans	Subcutaneous, connective tissue	Unknown
Pelecitus mazzanti	Pigeons	Subcutaneous, connective tissue	Unknown
Pelecitus scapiceps (syn. *Dirofilaria scapiceps*, *Loaina scapiceps*)	Rabbits, hares	Synovial sheaths of the feet	Species of mosquitoes

Chandlerella

Members of this genus are filarioid worms of birds. The main species is *Chandlerella quiscali* which infects the brain of emus and wild birds. This parasite has midges (*Culicoides* spp.) as intermediate hosts.

Chandlerella quiscali

Description: Slender worms, with males 8–15 mm and female worms 17–24 mm in length. In the male, the spicules are thick and equal in length and there are 3–4 pairs of postanal papillae.

Setaria

The members of this genus are usually harmless inhabitants of the peritoneal and pleural cavities (Table 1.43). The worms are slender and whitish, up to 12 cm long, and the posterior end is spirally coiled. The mouth is surrounded by a cuticular ring with dorsal, ventral and frequently lateral prominences, which give the worms a characteristic appearance. The tail of the male has four pairs of precloacal and usually four pairs of postcloacal papillae. The spicules are dissimilar and unequal in length. The tail of female worms usually has spines of several large conical projections. The site and gross appearance are sufficient for generic identification (Fig. 1.81).

Table 1.43 *Setaria* species.

Species	Hosts	Site	Intermediate hosts
Setaria congolensis (syn. *Setaria bernardi*)	Pigs	Peritoneum, pleural cavity	Mosquitoes
Setaria equina	Horses, donkeys, other equids	Peritoneum, pleural cavity	Mosquitoes
Setaria labiato-papillosa (syn. *Setaria digitata*, *Setaria altaica*, *Setaria cervi*)	Cattle, buffalo, bison, yaks, deer, antelopes, rarely sheep	Peritoneum, pleural cavity	Mosquitoes
Setaria digitatus	Cattle, buffalo	Peritoneum, pleural cavity	Mosquitoes

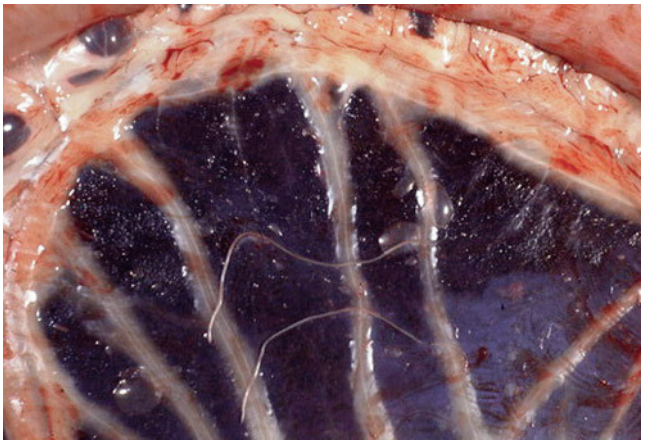


Fig. 1.81 *Setaria labiato-papillosa* in bovine mesentery.

Setaria congolensis

Synonym: *Setaria bernardi*

Description: Male worms are 8 cm and female worms 11–14 cm in length. The male worm has three pairs of small precloacal papillae and four pairs of large postcloacal papillae. The right spicule is spiny and the left spicule is comparatively long with a flagellated end.

Setaria equina

Description: The adults are long and slender with cephalic papillae. Males measure 8–10 cm and females 13–15 cm in length. Worms have an elevated chitinous peribuccal ring. The spiral tail of the female terminates in a point. Male spicules are unequal, the left being about three times longer than the right. The microfilariae present in the blood are sheathed and measure about 190–256 µm in length.

Life cycle: Larvae produced by adult worms in the body cavity circulate in the blood and are taken up by culicine mosquitoes, including *Aedes* and *Culex* species. Infective larvae develop in the mosquito muscles in two weeks and are reinjected into horses when the mosquitoes feed. The prepatent period is 8–10 months.

Setaria labiato-papillosa

Synonyms: *Setaria digitata*, *Setaria altaica*, *Setaria cervi*

Description: Males are 40–60 mm and females 60–120 mm in length. The dorsal and ventral prominences and the peribuccal ring are clearly perceptible. The tail of the female ends in a marked button, which is divided into a number of papillae. The male spicules are of unequal length, the left being around 2.5 times longer than the right. Microfilariae are sheathed and measure 240–260 µm.

Life cycle: Larvae produced by adult worms in the body cavity circulate in the blood and are taken up by culicine mosquitoes, including *Aedes* and *Culex* species. Infective larvae develop in the mosquito muscles in 12–16 days, and are reinjected into the final host when the mosquitoes feed. The prepatent period is 8–10 months.

Elaeophora

These long slender worms inhabit large blood vessels but are generally of local importance, leading to filarial dermatosis caused by circulating microfilariae (Table 1.44).

Table 1.44 *Elaeophora* species.

Species	Hosts	Site	Intermediate hosts
Elaeophora poeli	Cattle, buffalo, zebus	Aorta	Unknown
Elaeophora schneideri	Deer, sheep, goats	Blood vessels	Tabanid flies
Elaeophora bohmi	Horses	Blood vessels	Unknown

Elaeophora poeli

Description: Slender worms, males measuring around 4–7 cm and females up to 30 cm in length. The oesophagus is very long and lips are absent. The tail of the male possesses 5–7 pairs of papillae, of which two pairs are precloacal. Spicules are short and robust. Microfilariae are 340–360 µm.

Life cycle: The life cycle is indirect. The microfilariae are ingested by the intermediate host and the L_3, when developed, are released into the wound made when the insect next feeds. The male occurs in nodules in the wall of the aorta, while the female is fixed in nodules by its anterior extremity with the rest of the body free in the lumen of the aorta. Microfilariae occur in the blood and in subcutaneous connective tissue.

Elaeophora schneideri

Description: Slender worms; males are around 5–8 cm and females up to 12 cm long with a very long oesophagus. The tail of the male is coiled and the spicules are long, slender and unequal. Microfilariae are 270 µm, bluntly rounded anteriorly and tapering posteriorly.

Life cycle: Similar to *E. poeli*. Early development in the host appears to be in the meningeal arteries, then the worms migrate to the carotid arteries and are mature and producing microfilariae about 4.5 months after infection. The adult worms are embedded in the arterial intima of the carotid, mesenteric and iliac arteries; occasionally they are found in the digital and tibial arteries with only the anterior part of the female free in the lumen. The prepatent period is around 4–5 months.

Elaeophora bohmi

Description: These are slender worms, the males measuring 4.5–6 cm and females 4–20 cm in length. Microfilariae are 230–290 µm with a long tail.

Life cycle: The microfilariae are ingested by the intermediate host (tabanid flies) when blood feeding and the L_3, when developed, are released into the wound made when the insect next feeds. Microfilariae occur in the blood and in subcutaneous connective tissue.

Splendidofilaria

Parasites of birds, characterised by a relatively long tail and subequal spicules. The main species is *Splendidofilaria fallisensis* (syn. *Ornithofilaria fallisensis*) which infects the subcutaneous tissue of ducks. This parasite has slugs and blackflies (*Simulium*) as intermediate hosts.

Splendidofilaria fallisensis

Synonym: *Ornithofilaria fallisensis*

Description: These are delicate transparent nematodes, with male worms measuring 9–15 mm and female worms 24–40 mm in length.

Paronchocerca

This genus of filarial heartworms is of little veterinary importance. *Paronchocerca struthionis* has been reported in ostriches and rheas; *Paronchocerca ciconarum* has been reported to cause myocardial degeneration in storks. Intermediate hosts are unknown.

Paronchocerca struthionis

Description: Long abursate nematodes, 3–5 cm in length with bluntly rounded extremities. Male spicules are dissimilar in length; a gubernaculum is absent.

Filariosis in humans

Filarioid worms are probably the most important group of helminth infections in humans, but are of only marginal concern to the veterinarian since domestic animals are of little significance in their epidemiology. Of greatest importance in human medicine are the genera *Onchocerca*, *Brugia*, *Loa*, *Wuchereria* and *Mansonella*.

1. *Onchocerca volvulus*: Human onchocercosis, due to *O. volvulus*, occurs around the world in the equatorial zone and is transmitted by *Simulium* spp. (blackflies). The adult worms live in subcutaneous nodules, and almost the entire pathogenic effect is caused by the microfilariae; dermatitis and elephantiasis are common, but the most important effect is ocular onchocercosis ('river blindness'), so called because of its distribution along the habitats of *Simulium* spp. Dying microfilariae cause a sclerosing keratitis in the cornea that leads to corneal opacification and retinochoroiditis. It has been estimated that in Africa, about 20 million people are affected by onchocercosis. The only other animals to which it is transmissible are the higher primates, chimpanzee and gorilla. Ivermectin is effective in reducing skin microfilarial counts in *O. volvulus* infection and repeated treatment should help reduce transmission. The onchocercosis-associated pathology in the eye and skin has also been shown to be reduced with ivermectin treatment.
2. *Brugia* spp. are carried by many species of mosquito and occur in Southeast Asia, notably in Malaysia, causing elephantiasis. The most important species, *B. malayi*, is also infective for monkeys and domestic and wild carnivores, and has been transmitted experimentally to the cat and dog. The lesser species occurring in human, *B. pahangi*, has a reservoir in many species of domestic and wild animals, including the dog and cat. Adult parasites inhabit lymph nodes and afferent lymphatic vessels.
3. *Wuchereria bancrofti* is also mosquito borne and affects the lymphatic system, causing elephantiasis in Africa, Asia and South America. It is exclusive to humans. As with *Brugia* spp., the main pathogenic effects are associated with adult worms rather than with microfilariae.
4. *Loa loa* is transmitted by *Chrysops* spp. (tabanid flies), and occurs in West, Central and East Africa, where it causes the transient subcutaneous enlargements known as 'Calabar swellings'. It is confined to humans, apes and monkeys. Longevity can be up to 20 years.
5. *Mansonella ozzardi*, carried by *Culicoides* and *Simulium* spp., occurs in the Caribbean and Central and South America. It lives in the fat and on the mesentery or pleural cavity, and is usually considered to be non-pathogenic, though recently it has been associated with allergic signs. The prevalence is extremely high in endemic areas, where parasites closely resembling *M. ozzardi* are commonly found in monkeys, horses and cattle. However, there is reluctance to presume that these animals may be reservoir hosts until positive identification is made.

CLASS ENOPLEA

ORDER ENOPLIDA

SUPERFAMILY TRICHUROIDEA

The members of this superfamily are found in a wide variety of domestic animals. A common morphological feature is the 'stichosome' oesophagus that is composed of a capillary-like tube surrounded by a single column of cells. The male has only one spicule within a sheath, or it may be completely absent (e.g. *Trichinella*). There are several genera of veterinary interest in the family Trichuridae. The Trichuridae include species of *Trichuris*, which are found in the caecum and colon of mammals; *Capillaria* (*Eucoleus*) species are most commonly present in the alimentary or respiratory tract of mammals or birds. Both lay eggs with plugs at both poles. *Trichosomoides* species are bladder worms found in rodents and are of minor interest. *Anatrichosoma* are parasites of primates, occasionally reported in humans, and are found in the skin and nasal passages.

FAMILY TRICHURIDAE

Trichuris

Worms belonging to this genus are commonly known as 'Whipworms' because the thick broad posterior end tapers rapidly to a long filamentous anterior end (about twice as long as the posterior region) that is characteristically embedded in the mucosa (Fig. 1.82; Table 1.45). The anterior of the worm bears a small point. The male tail is tightly coiled and possesses a single spicule in a protrusible sheath.

Fig. 1.82 *Trichuris suis* adult worms.

Table 1.45 *Trichuris* species.

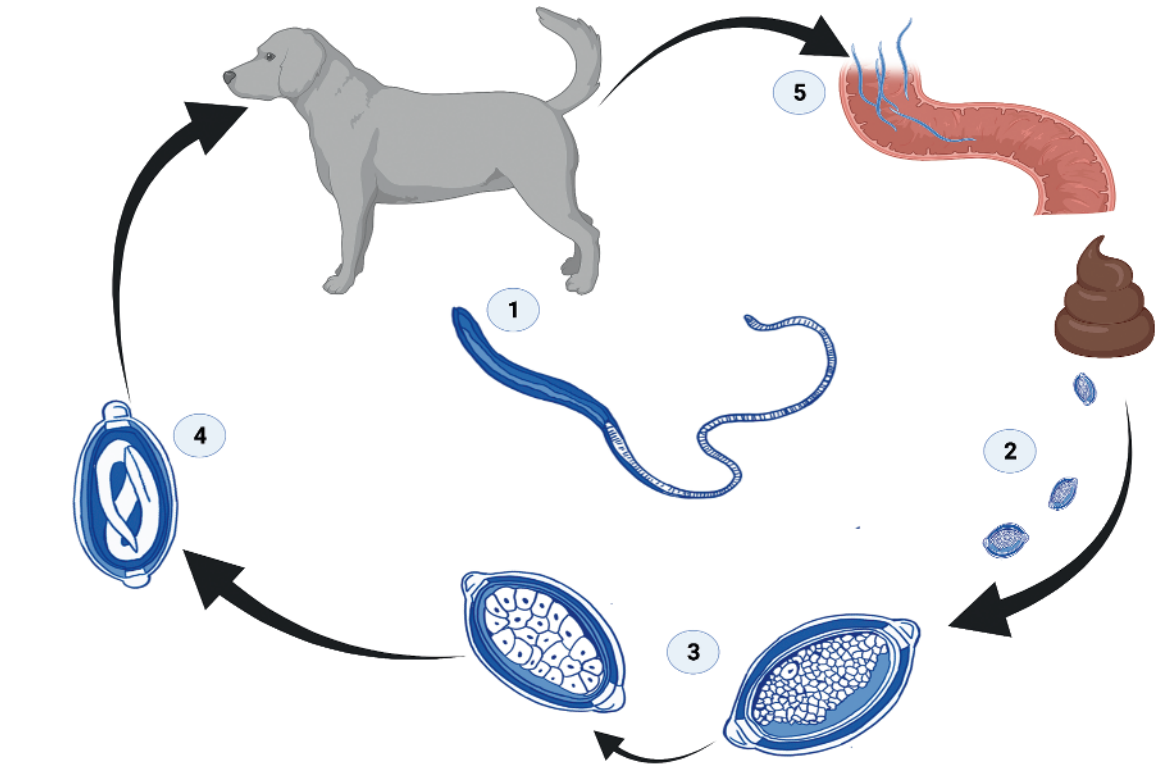
Species	Hosts	Site
Trichuris campanula	Cats	Large intestine
Trichuris capreoli	Deer	Large intestine
Trichuris discolor	Cattle, buffalo, occasionally sheep, goats	Large intestine
Trichuris globulosa	Cattle, occasionally sheep, goats, camels, other ruminants	Large intestine
Trichuris leporis	Rabbits, hares, coypus	Large intestine
Trichuris muris	Rats, mice	Large intestine
Trichuris ovis	Sheep, goat, occasionally cattle and other ruminants	Large intestine
Trichuris serrata	Cats	Large intestine
Trichuris skrjabini	Sheep, goats, camels	Large intestine
Trichuris suis	Pigs, wild boar	Large intestine
Trichuris trichiura	Humans, primates	Large intestine
Trichuris vulpis	Dogs, foxes, cats	Large intestine
Trichuris cameli	Camels	Large intestine
Trichuris tenuis	Llamas, alpacas	Large intestine

Trichuris trichiura, the whipworm of human and simian primates, is morphologically indistinguishable from *T. suis*. However, it is generally considered that these two parasites are strictly host specific. Worldwide, the number of cases in humans is several hundred million, with around 10 000 deaths per year attributed to trichuriosis. It is more common in children. The taxonomic status of *Trichuris* species is very confused because many described species may be synonymous, reflecting the fact that an accepted species has been found in a different host and determined as a new species.

Life cycle: The infective stage is the L_1 within the egg, which develops within 1–2 months of being passed in the faeces, depending on the temperature. Under optimal conditions, these larvated eggs may subsequently survive and remain viable for several years. After ingestion, the plugs are digested and the released L_1 penetrate the mucosal glands of the distal ileum, caecum and colon. Subsequently, all four moults occur within these glands, the adults emerging to lie on the mucosal surface with their anterior ends embedded in the mucosa. The prepatent period is about 7–10 weeks. See **life cycle 16**.

LIFE CYCLE 16. LIFE CYCLE OF *TRICHURIS VULPIS*

Adults of *Trichuris vulpis* (1) live in the caecum and colon of the dog. After mating, the females release elliptical eggs, characteristically lemon-shaped, defined by the presence of 'polar plugs' at each end (2). The eggs are non-segmented and are eliminated in the external environment with the faeces, where they mature (3) until an infective first-stage larva (L_1) forms inside each egg (4). The dog acquires the infection by ingesting larvated eggs. After hatching in the intestinal lumen, the larvae begin migrating through the mucosa. After 8–10 days, the larvae return to the intestinal lumen (5), attach to the mucosa with their cephalic end and develop into sexually mature adults (1).



Made by Jairo Mendoza-Roldan (University of Bari, Italy) in bio RENDER

Trichuris discolor

Description: Worms are similar to *T. globulosa* but the females are yellow-orange in colour. Eggs measure about 65 by 30 µm.

Trichuris globulosa

Description: The adults are long white worms, with males measuring 4–7 cm and females 4–6 cm in length. The single spicule sheath bears a terminal spherical expansion, on which are spines larger than on the rest of the sheath. The male tail is coiled and possesses a single spicule in a protrusible sheath. The sheath is covered with minute spines and bears a spherical appendage; the female tail is merely curved. The characteristic medium-sized eggs are lemon-shaped, 70–80 by 30–40 µm, with a thick smooth shell and a conspicuous protruding transparent polar plug (operculum) at both ends. The content of the egg is granular, there being no blastomeres. In the faeces these eggs appear yellowish or brown in colour.

Trichuris leporis

Description: Adult males measure 1.9–2.1 cm and adult females 1.7–2.1 cm in length.

Trichuris ovis

Description: The adults are long white worms, the males measuring 5–8 cm and the females 3.5–7 cm in length with a thick broad posterior end tapering rapidly to a long filamentous anterior end that is characteristically embedded in the mucosa. The male tail is coiled and possesses a single spicule in a protrusible sheath. The sheath bears an oblong swelling a short distance from its distal extremity and is covered with minute spines, which decrease in size towards the distal end. The female tail is merely curved. The characteristic eggs are lemon-shaped, with a thick smooth shell and a conspicuous protruding transparent polar plug (operculum) at both ends (see Fig. 4.4). In the faeces these eggs appear yellow or brown in colour. They measure around 70–80 by 30–42 µm and when laid, they contain an unsegmented embryo.

Trichuris skrjabini

Description: Males of *T. skrjabini* have one short spicule (0.82 mm) with a rounded tip that is always fully covered by the spicule sheath and large conical caudal papillae.

Trichuris suis

Description: The adults are whitish and about 3–5 cm long with a thick broad posterior end tapering rapidly to a long filamentous anterior end that is characteristically embedded in the mucosa (Fig. 1.83). The male tail is coiled and possesses a single spicule in a protrusible sheath. The sheath is variable in shape and in the extent of its spinous armature. The female tail is curved. The characteristic eggs are lemon-shaped, 50–68 by 21–31 µm, with a thick smooth shell and a conspicuous transparent protruding polar plug at both ends; in the faeces these eggs appear yellow or brown in colour. The contents are granular, unsegmented and brownish.

Fig. 1.83 *Trichuris suis* on the surface of the large intestine.

Trichuris trichiura

Description: Females are slightly larger than male worms (approximately 3.5–5 cm compared to 3–4.5 cm). The females have a bluntly round posterior compared to their male counterparts with a coiled posterior end.

Trichuris vulpis

Description: The adults are whitish and about 4.5–7.5 cm long with a thick broad posterior end tapering rapidly to a long filamentous anterior end that is characteristically embedded in the mucosa (Fig. 1.84). The male tail is coiled and possesses a single spicule in a protrusible sheath. The sheath bears small spines only on its anterior portion. The characteristic eggs are lemon-shaped, with a thick smooth shell, slightly barrel-shaped side walls and conspicuous protruding transparent polar plugs at both ends. They measure 80–90 by 36–42 µm and in the faeces these eggs appear yellow or brown in colour with granular unsegmented contents (see Fig. 4.7).

Fig. 1.84 *Trichuris vulpis* adults recovered from an infected intestine.

Trichosomoides

These are permanent hyperparasites that inhabit the urinary bladder of rats.

Life cycle: Infection is by ingestion of embryonated eggs voided in the urine. Eggs hatch in the stomach, penetrate the stomach wall and are carried in the blood to the lungs and other parts of the body. Only those larvae that reach the kidneys or urinary bladder survive. The life cycle takes 8–9 weeks and the prepatent period is 8–12 weeks. The main species is *Trichosomoides crassicauda* which infects the bladder of rats.

Trichosomoides crassicauda

Description: The female is 10–19 mm long; the male measures 1.5–3.5 mm and is a permanent hyperparasite living within the reproductive tract of the female. The medium-sized egg is lemon-shaped with protruding transparent polar plugs and measures about 60–70 by 30–36 µm. The shell is thick and brown in colour, and contains either a morula or an L_1 larva. Eggs are only found in the urine.

Anatrichosoma

Members of this genus have been reported from the skin and nasal mucosa of primates and the skin and mucosa of wild rodents and marsupials. There have been some reports of infections with species of these parasites in dogs, cats and humans.

FAMILY CAPILLARIIDAE

Capillaria

Worms belonging to this genus, commonly known as 'Hairworms' or 'Threadworms', are very fine whitish filamentous worms, the narrow stichosome oesophagus occupying about one-third to half the body length (Table 1.46). There is a simple mouth and a buccal capsule is absent. The males have a long thin colourless single spicule and often possess a primitive bursa-like structure. The small eggs are slightly lemon-shaped (similar to *Trichuris*) but the side walls are almost parallel. They measure 45–50 by 22–25 µm, are colourless and have thick shells that are slightly striated with two protruding transparent bipolar plugs. The contents are granular with no blastomeres.

Life cycle: The life cycles are generally direct but some species found in birds have indirect life cycles, with earthworms acting as intermediate hosts. The infective L_1 develops within the egg in about 3–4 weeks. Infection of the final host is through ingestion of this embryonated infective stage and development to adult worms occurs usually without a migration phase. The taxonomy and systematics of these parasites have been changed many times because of a difficulty in designation of particular species' features and there are many synonyms in this group. Some species of *Capillaria* are now listed under the generic name *Eucoleus*, although they may universally still be referred to as *Capillaria*.

Capillaria anatis

Synonyms: *Capillaria brevicollis*, *Capillaria collaris*, *Capillaria mergi*, *Thornix anatis*

Table 1.46 *Capillaria/Eucoleus* species.

Species	Hosts	Site
Capillaria anatis (syn. *Capillaria brevicollis*, *Capillaria collaris*, *Capillaria mergi*, *Thornix anatis*)	Chickens, turkeys, gallinaceous birds (pheasants, partridges), pigeons, ducks, geese	Caeca
Capillaria anseris (syn. *Baruscapillaria anseris*)	Geese, ducks	Small intestine
Capillaria bovis (syn. *Capillaria brevipes*)	Cattle	Small intestine
Capillaria bilobata	Zebus	Abomasum
Capillaria bursata	Chickens, turkeys, pheasants, ducks and wild birds Intermediate hosts: earthworms	Small intestine
Capillaria caudinflata (syn. *Aonchotheca caudinflata*)	Chickens, turkeys, geese, pigeons and wild birds Intermediate hosts: earthworms	Small intestine
Capillaria feliscati (syn. *Pearsonema feliscati*)	Cats	Bladder
Capillaria hepatica (syn. *Callodium hepatica*, *Hepaticola hepatica*)	Rats, mice, squirrels, rabbits and farmed mustelids; occasionally dogs, cats, humans, primates	Liver
Capillaria longipes	Sheep, goat, cattle	Small intestine
Capillaria obsignata (syn. *Baruscapillaria obsignata*, *Capillaria columbae*)	Pigeons, chickens, turkeys, pheasants and wild birds	Small intestine
Capillaria phasianina (syn. *Thornix phasianina*)	Pheasants, grey partridges	Small intestine, caecae
Capillaria philippinensis	Humans	Small intestine
Capillaria plica (syn. *Pearsonema plica*)	Dogs, cats, foxes, wolves	Bladder
Capillaria putorii (syn. *Aonchotheca putorii*)	Cats, dogs, mustelids, hedgehogs, bears, raccoons	Stomach, small intestine
Capillaria uropapillata	Pheasants	Oesophagus, crop
Eucoleus aerophila (syn. *Capillaria aerophila*)	Foxes, mustelids, occasionally dogs, coyotes, cats and humans	Trachea, bronchi
Eucoleus boehmi (syn. *Capillaria boehmi*)	Foxes, dogs	Nasal, frontal and maxillary sinuses
Eucoleus annulata (syn. *Capillaria annulata*)	Chickens, turkeys, ducks and wild birds Intermediate hosts: earthworms	Oesophagus, crop
Eucoleus contorta (syn. *Capillaria contorta*)	Chickens, turkeys, pheasants, ducks and wild birds Intermediate hosts: earthworms	Oesophagus, crop
Eucoleus perforans (syn. *Capillaria perforans*)	Pheasants, guinea fowls	Oesophagus, crop

Description: Males measure around 16–24 mm and females 28–38 mm in length. The males have a long thin single spicule and often possess a primitive bursa-like structure. The eggs are slightly barrel-shaped, light brown and with protruding transparent polar plugs (see Fig. 4.8). They measure around 48–65 by 23–35 µm and the outer shell is thick, striated and rugose. More details of the eggs are given under *Capillaria contorta*.

Life cycle: The life cycle is direct. The infective L_1 develops within the egg in about 3–4 weeks. Infection of the final host is through ingestion of this embryonated infective stage, and development to adult worms occurs without a migration phase. The prepatent period is 3–4 weeks.

Capillaria bursata

Description: Males measure around 6–12 mm and females up to 25 mm.

Life cycle: The life cycle of this species is indirect.

Capillaria bovis

Synonym: *Capillaria brevipes*

Description: Males measure around 8–9 mm and females up to 12 mm.

Capillaria caudinflata

Synonym: *Aonchotheca caudinflata*

Description: See *Eucoleus annulata*. Males measure around 6–12 mm and females up to 25 mm. Females have a characteristic projecting vulval appendage. The medium-sized eggs measure 43–69 by 20–27 µm and have a finely sculptured thick shell; their other characteristics are more fully described under *Eucoleus contorta*.

Life cycle: The life cycle of this species is indirect.

Capillaria hepatica

Synonyms: *Callodium hepatica*, *Hepaticola hepatica*

Description: These are very fine filamentous worms generally measuring 10–50 mm in length. The males have a long thin single spicule and often possess a primitive bursa-like structure. The medium-sized eggs are barrel-shaped and almost colourless. They have thick shells that are slightly striated with minute pores and the bipolar plugs protrude. Eggs measure about 48–62 by 29–37 µm and contain a morula.

Life cycle: The life cycle is direct and differs from that of other *Capillaria* species. Adult *C. hepatica* worms reproduce in the liver and females lay groups of eggs in the parenchyma where they become encapsulated by the host's reaction. These eggs are therefore not released directly from the host. Infection is acquired by ingestion of either the liver, following predation, cannibalism or carrion feeding, or eggs on the ground, which have been freed by decomposition of the host. Eggs in the soil will embryonate and be infective in about four weeks. When infective eggs are ingested by the host, they hatch in the intestine and the larvae penetrate the intestinal wall and are carried to the liver via the lymphatics and the bloodstream.

Capillaria longipes

Description: These are very fine filamentous worms, the narrow stichosome oesophagus occupying about one-third to half the body length. Males measure around 10–13 mm and females up to 20 mm. The males have a long thin single spicule, 1.2 mm long, and often possess a primitive bursa-like structure. The females contain eggs that resemble those of *Trichuris* in possessing bipolar plugs. The eggs are only slightly barrel-shaped, the midregions of the shell wall being parallel. They measure 45–50 by 22–25 µm and are colourless, and have thick shells that are slightly striated with slightly projecting transparent bipolar plugs (see Fig. 4.4).

Life cycle: The prepatent period is 3–4 weeks.

Capillaria obsignata

Synonyms: *Baruscapillaria obsignata*, *Capillaria columbae*

Description: See *Eucoleus annulata*. Males measure around 10–12 mm and females up to 15 mm in length. The tail of the female worm tapers posteriorly. The medium-sized eggs are barrel-shaped with slightly striated bipolar plugs and possess a shell with a reticulate pattern. They measure around 50–62 by 20–25 µm; their other characteristics are more fully described under *Eucoleus contorta*.

Life cycle: This species has a direct life cycle. The infective L_1 develops within the egg in about 7–10 days. Infection of the final host is through ingestion of this embryonated infective stage, and development to adult worms occurs without a migration phase. The prepatent period is around three weeks.

Capillaria plica

Synonym: *Pearsonema plica*

Description: Fine, whitish, filamentous worms 1–6 cm long; males measure 13–30 mm and females 30–60 mm. The males have a long thin single spicule and often possess a primitive bursa-like structure. The medium-sized ovoid eggs are barrel-shaped, and have thick yellowish shells that are slightly striated with protruding transparent flattened bipolar plugs. They measure 63–68 by 24–27 µm and the almost colourless contents are granular and unsegmented. The egg is only observed in urine.

Life cycle: This parasite requires an earthworm intermediate host, ingested eggs developing to the infective L_3 within 30 days. The prepatent period is around eight weeks.

Capillaria feliscati

Synonym: *Pearsonema feliscati*

Description: Adult worms are small thread-like parasites; adult females measure 30–60 mm, males 13–30 mm long. Eggs are oval and colourless with a thick capsule and typical bipolar plugs, and measure 50–68 by 22–32 µm.

Capillaria putorii

Synonym: *Aonchotheca putorii*

Description: Thin filamentous worms, about 10 mm long; males are 5–8 mm and females 9–15 mm. The medium-sized, oval, elongate eggs have broad flat poles with two protruding semi-transparent polar plugs. They measure around 60 by 30 µm and contain granular unsegmented contents.

Eucoleus aerophila

Synonym: *Capillaria aerophila*

Description: These are very fine, whitish, filamentous worms, the narrow stichosome oesophagus occupying about one-third to half the body length. Males measure around 24 mm and females 32 mm. The males have a long thin single spicule and often possess a primitive bursa-like structure. The females contain eggs that resemble those of *Trichuris* in possessing bipolar plugs. The elongate, oval, medium-sized eggs are barrel-shaped and possess a thick, granular, slightly striated shell. The poles of each egg have a protruding transparent plug. Eggs measure about 59–80 by 30–40 µm and have a greenish to yellowish-brown colour and contain granular unsegmented contents. These eggs can be differentiated from those of *Trichuris vulpis*, which are larger and possess a smooth shell, and from those of *Capillaria plica*, which are almost colourless and are passed in the urine.

Eucoleus boehmi

Synonym: *Capillaria boehmi*

Description: These are fine, whitish, filamentous worms with adults measuring 15–40 mm long. The males have a long thin single spicule. The females contain eggs that macroscopically resemble those of *E. aerophila* in possessing bipolar plugs. Microscopically, the eggs can be differentiated: the surface of *E. boehmi* eggs are pitted whereas those of *E. aerophila* are covered with a network of branching ridges.

Eucoleus annulata

Synonym: *Capillaria annulata*

Description: These are very fine filamentous worms, the narrow stichosome oesophagus occupying about one-third to half the body length. Males measure around 15–25 mm and females 37–80 mm. The males have a long thin single spicule, with a spiny spicule sheath, and often possess a primitive bursa-like structure. This species has a cuticular swelling at the back of the head. The females contain eggs that resemble those of *Trichuris* in possessing bipolar plugs. The medium-sized eggs are barrel-shaped and colourless to pale brown, 60–65 by 25–28 µm, and have thick shells that are slightly striated with bipolar plugs.

Life cycle: The life cycle is indirect. Eggs passed in faeces are ingested by earthworms and develop to the infective stage in 2–3 weeks. The prepatent period is about 3–4 weeks in the final host.

Eucoleus contorta

Synonym: *Capillaria contorta*

Description: General description as for other *Eucoleus/Capillaria* species. Males measure around 12–17 mm and females 27–38 mm. The medium-sized lemon-shaped eggs measure about 48–60 by 21–28 µm. They have slightly barrel-shaped asymmetrical side walls with protruding transparent polar plugs. Eggs have a thick brown shell with a smooth surface and their granular contents are unsegmented.

Life cycle: *Eucoleus contorta* appears to be able to develop both directly and indirectly. In the direct life cycle, the infective L_1 develops within the egg in about 3–4 weeks. Infection of the final host is through ingestion of this embryonated infective stage, and development to adult worms occurs without a migration phase. In the indirect life cycle, the egg needs to be ingested by an earthworm in which it hatches, the final host being infected by ingestion of the earthworm. The prepatent period is about 3–4 weeks in the final host.

Capillariosis in humans

Three species of *Capillaria*, *C. philippinensis*, *C. hepatica* and *Eucoleus* (*Capillaria*) *aerophila*, can infect humans. Humans acquire *C. hepatica* infection through ingestion of soil containing embryonated eggs or by consuming contaminated food or water. Heavy infections in human induce similar hepatic lesions to those seen in other mammalian hosts and hepatic capillariosis is usually fatal.

Capillaria philippinensis infects the small intestine and causes a severe enteropathy that can be fatal. It occurs mainly in the Philippines and Thailand, with sporadic outbreaks in other parts of Southeast Asia, India, the Middle East and southern Europe. Eggs shed into water embryonate and are ingested by freshwater or brackish-water fish and develop to the infective stage in the intestinal mucosa. Infection is acquired through the consumption of raw or undercooked fish. Large infections can accumulate through autoinfection. Fish-eating birds are thought to be the reservoir host. Clinical signs include intermittent diarrhoea, followed by anorexia, abdominal distension and weight loss. There is a protein-losing enteropathy. Human capillariosis resulting from *E. aerophila* is very rare.

SUPERFAMILY TRICHINELLOIDEA

FAMILY TRICHINELLIDAE

Trichinella are found in the small intestine of mammals and produce larvae that immediately invade the tissues of the same host.

Trichinella

The taxonomy of the genus has been controversial until very recently. It is composed of several sibling species that cannot be differentiated morphologically but molecular typing, and other criteria, have now identified eight species of *Trichinella* (Table 1.47).

Table 1.47 *Trichinella* species.

Species	Distribution	Principal hosts	Resistance to freezing
Capsule forming			
Trichinella spiralis	Cosmopolitan	Pigs, rats, horses, wide range of mammals, humans	No
Trichinella nativa	Arctic and subarctic zones: North America, Finland, Sweden	Wild carnivores, seals, polar bears, walruses	High
Trichinella nelsoni	Tropical Africa	Wild carnivores and omnivores	No
Trichinella britovi	Temperate zone of Palaearctic region	Wild carnivores, foxes, wild boar, horses, humans	Low
Trichinella murrelli	North America	Wildlife, horses, humans	No
Non-capsule forming			
Trichinella pseudospiralis	Cosmopolitan	Mammals, birds	No
Trichinella papuae	Papua New Guinea	Wild pigs, humans	No
Trichinella zimbabwensis	Zimbabwe	Crocodiles	No

Description: Because of their short lifespan, the adult worms are rarely found in natural infections. The male is about 1.5 mm and the female 3.5–4 mm long. The oesophagus is at least one-third of the total body length, and the tail in the male has two small knob-shaped conical cloacal flaps but no copulatory spicule nor a spicule sheath. In the female, the uterus contains developing larvae. The vulva is sited in the midoesophageal region of the worm. *Trichinella* infection is most easily identified by the presence of coiled larvae in striated muscle (Fig. 1.85). These larvae measure about 800–1000 µm in length. The cysts are lemon-shaped, 0.3–0.8 by 0.2–0.4 mm in size and often transparent. Adult worms are unlikely to be encountered during gross examination of intestinal digesta.

Life cycle: The life cycle is indirect. The adult parasites and infective larvae (muscle trichinae) are unusual in being present within a single host (i.e. development from larva to adult to larva in a single host). *Trichinella* does not have a free-living stage. The very small developing adults lie between the villi of the small intestine. After fertilisation, the males die while the females burrow deeper into the intestinal mucosa. About a week later, they produce L_1 which enter the lymphatic vessels and travel via the bloodstream to the skeletal muscles. There, still as L_1, they penetrate striated muscle cells where they are encapsulated by the host, grow and assume a characteristic coiled position; the parasitised muscle cell is transformed by microvascularisation into a 'nurse cell'. This process is complete within about 3–4 weeks, by which time the larvae are infective and may remain so for many years. Development is resumed when muscle, containing the encysted trichinae, is ingested by another host, usually as a result of predation or carrion feeding. The L_1 is liberated in the stomach and in the intestine undergoes four moults to become sexually mature within about a week. Patent infections persist for only a few weeks at the most. See **life cycle 17**.

SUPERFAMILY DIOCTOPHYMATOIDEA

This group contains three genera: *Dioctophyma*, found in the kidney of carnivores, and *Hystrichis* and *Eustrongyloides*, which occur in aquatic fowl. The alimentary canal is attached to the abdominal wall by four longitudinal muscles and the tail of the male has a terminal cup-shaped bursa which lacks bursal rays. A single spicule is present.

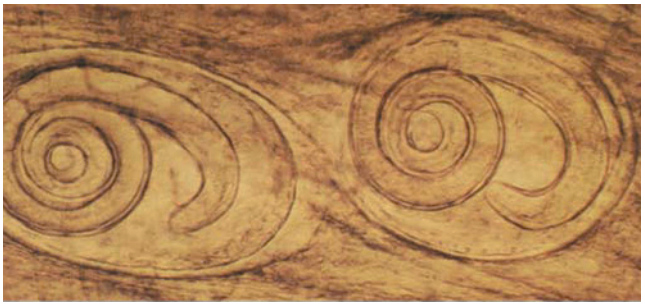


Fig. 1.85 Coiled infective larvae of *Trichinella spiralis* in striated muscle.

FAMILY DIOCTOPHYMATIDAE

Dioctophyma

Dioctophyma renale (syn. *Dictophyme renale*, *Eustrongylus gigas*), 'kidney worm', is the largest parasitic nematode known in domestic animals and is found in the abdominal cavity and kidneys of dogs, foxes, mink, ferrets, otters, pine martens, polecats andseals, occasionally in cats, pigs, horses and humans. This parasite has aquatic oligochaetes (annelids) as intermediate hosts.

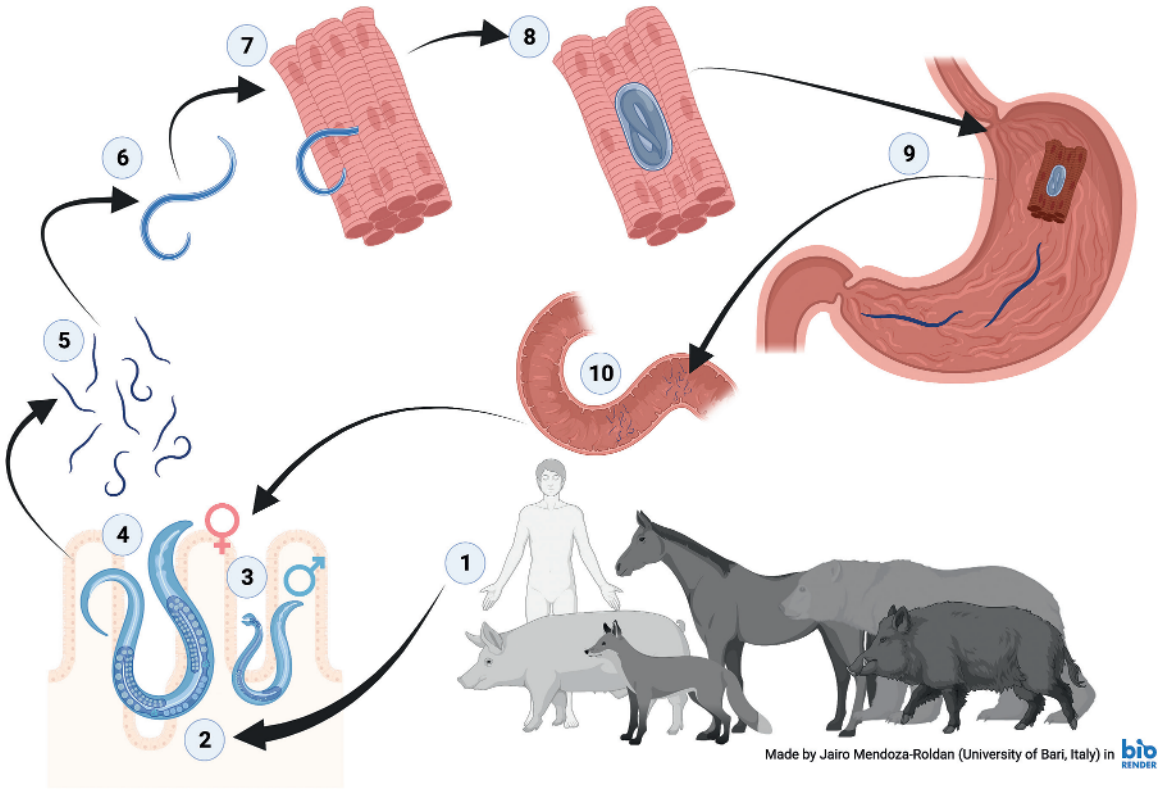
Dioctophyma renale

Synonym: *Dictophyme renale*, *Eustrongylus gigas*

Description: Female worms usually measure more than 60 cm in length, with a diameter of around 1 cm but can occasionally be as long as 100 cm. The male is about 35–40 cm long with a bell-shaped bursa which is lined with papillae and a supporting ray is absent (Fig. 1.86). A single brown spicule is present. The worms are deep red–purple in colour. Their size and predilection site are sufficient for identification. Male worms have only one spicule and possess a bell-shaped copulatory bursa. The eggs are lemon-shaped, yellowish-brown, with a thick pitted shell and slightly protruding bipolar plugs. They measure about 71–84 by 46–52 µm and the granular contents are unsegmented when passed. The eggs are observed in the urine.

LIFE CYCLE 17. LIFE CYCLE OF *TRICHINELLA* SPP.

Trichinella spp. is the only genus of nematodes that completes its whole life cycle within a single host. These parasites infect the vast majority of mammalian species, including humans, and also birds and reptiles. Trichinellosis is regarded as a severe zoonosis, with an incidence varying widely between different countries. *Trichinella* spp. are common in wildlife, and infections have been reported in boars, foxes, bears, wolves, coyotes, badgers, lynx and small rodents, as well as pigs, horses and domestic carnivores. Thus, trichinellosis is an infection mostly occurring in sylvatic environments, and transmission to humans occurs via the ingestion of raw or undercooked game meat, or pig and horse meat from infected animals (1). Adult parasites live among the villi of the small intestine (2) and are rarely detected during natural infections as they are short-lived (six weeks at most). Males are 1.5 × 40 µm, with a well-developed oesophagus (over one-third of the whole-body length), without spicules but with a cloaca featuring two small 'flaps' (3). Females (3–4 mm × 60 µm) are viviparous (4). After mating, the males die, whilst the females travel deeper through the villi and, within 3–5 days, begin releasing L_1 (5). Within 4–16 weeks, females release up to 2000 larvae that penetrate the lymphatic system and, via the circulation, travel to the skeletal muscles, especially the diaphragm, masseter, tongue, extraocular, laryngeal and intercostal muscles. The larvae (6) (100 × 8 µm) feature a rounded tail, long oesophagus and an apical stiletto; on penetrating the muscular fibres (7), the larvae induce transformation of the latter into 'mother cells' (also known as 'nurse cells', 8). The L_1 grow and, without moulting, begin to coil ~18 days later. Due to the onset of reactive processes, a thin connective capsule forms around the cysts of some *Trichinella* species, with each larva encased in a structure resembling a lemon with groups of adipocytes deposited at each pole. Inside these cysts, the parasite remains alive and infective for long periods of time. Nevertheless, after ~6 months, a calcification process may begin around the cysts. Ingestion of infected meat by a new host allows the larvae to exit the cysts thanks to the activity of gastric juices (9), and to travel to the duodenum. Here, the L_1 undergo three moults (from L_1 to L_4, 10), and subsequent sexual development.



Life cycle: The worms are oviparous. The eggs, in the single-cell stage, are passed in the urine in clumps or chains and are ingested by the annelid intermediate host, in which the two preparasitic moults occur. The development phase in the annelid is about 2–4 months. The final host is infected by swallowing the annelid with the drinking water, or by the ingestion of a paratenic host, such as a frog or fish, which has itself eaten the infected annelid. In the final host, the infective larvae penetrate the intestinal wall, enter the peritoneal cavity and eventually penetrate the kidney. The prepatent period is about six months but has been observed to be as long as two years.

Hystrichis

The main species is *Hystrichis tricolor* which infects the proventriculus oesophagus of domestic and wild ducks and anatid birds. This parasite has aquatic oligochaetes (annelids) as intermediate hosts.

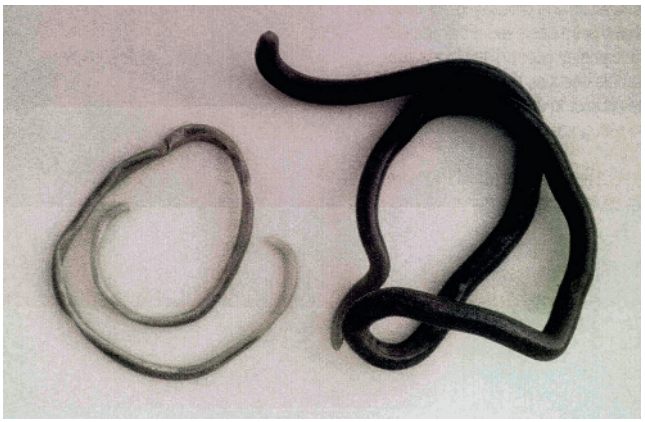


Fig. 1.86 Male and female worms of the kidney worm *Dioctophyma renale*.

Hystrichis tricolor

Description: Adult female worms are up to about 4 cm and males 2.5 cm in length. The cephalic area is expanded, and possesses many regularly positioned spines. The eggs are thick-shelled, coated with tubercles and have truncated poles. They measure about 85–88 by 36–40 µm and only develop slowly in water, taking around 8–9 weeks to reach the embryonated stage.

Life cycle: This is indirect. Fowl and other birds become parasitised through ingestion of infected oligochaetes. The adult worms are deeply embedded in the mucosa, with their caudal and cephalic regions lying within the lumen of the tract. The prepatent period is around two weeks.

Eustrongyloides

Parasites of waterfowl found in the oesophagus and proventriculus (Table 1.48).

Life cycle: The life cycles of *Eustrongyloides* species are not fully known but oligochaetes are likely to be involved as intermediate hosts and various fish as paratenic hosts.

Eustrongyloides papillosus

Description: Females measure about 3 cm in length. The male has a bursal cup with a fringed margin.

Eustrongyloides tubifex

Description: Males measure around 3–3.5 cm and females 3.5–4.5 cm in length. This worm has a small mouth and the head lacks spines. The cuticle is annulated. The male bursal cup is shaped like a trumpet and the spicule is slender and long.

Table 1.48 *Eustrongyloides* species.

Species	Hosts	Site	Intermediate hosts
Eustrongyloides papillosus	Ducks, geese	Proventriculus, oesophagus	Aquatic oligochaetes Fishes
Eustrongyloides tubifex (syn. *Strongylus tubifex*, *Eustrongylus tubifex*, *Hystrichis tubifex*)	Waterfowl	Proventriculus, oesophagus	Aquatic oligochaetes Fishes

PHYLUM ACANTHOCEPHALA

This is a separate phylum, closely related to the Nematoda, that contains a few genera of veterinary importance. They are generally referred to as 'thorny-headed worms' due to the presence of a hook-covered proboscis anteriorly (Fig. 1.87), and most are parasites of the alimentary tract of vertebrates. The body is usually cylindrical, although some are flattened. The hollow proboscis armed with recurved hooks, which aid in attachment, is retractable and lies in a sac. There is no alimentary canal, with absorption taking place through the thick cuticle, which is often folded and invaginated to increase the absorptive surface. The sexes are separate, males being much smaller than females. Posteriorly, the male has a muscular bursa and penis. After copulation, eggs, discharged by ovaries into the body cavity of the female, are fertilised and taken up by a complex structure called the uterine bell, which only allows mature eggs to pass out. These are spindle-shaped, thick-shelled and contain a larva which has an anterior circlet of hooks and spines on its surface and is called an **acanthor**.

Life cycle: The life cycle is indirect, involving either an aquatic or terrestrial arthropod intermediate host. On ingestion by the intermediate host, the egg hatches and the acanthor migrates to the haemocoel of the arthropod where it develops to become a **cystacanth** after 1–3 months. The definitive host is infected by ingestion of the arthropod intermediate host, and the cystacanth, which is really a young adult, attaches and grows to maturity in the alimentary canal. The prepatent period varies from five to 12 weeks.

FAMILY OLIGACANTHORHYNCHIDAE

The major genera of veterinary significance are *Macracanthorhynchus*, which is found in pigs, *Oncicola* found in dogs and other canids, and *Prosthenorchis* (*Oncicola*) which is found in primates.

Macracanthorhynchus

The main species is *Macracanthorhynchus hirudinaceus* which infects the small intestine of pigs and wild boar. This parasite has various dung beetles and water beetles as intermediate hosts.

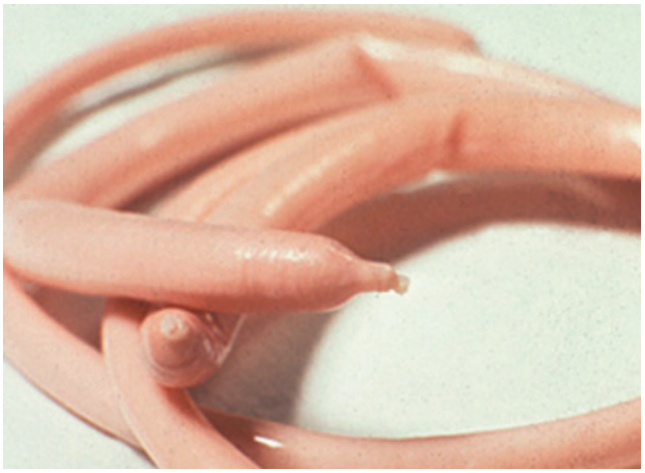


Fig. 1.87 Head of *Macracanthorhynchus hirudinaceus* showing the retractible proboscis.

Macracanthorhynchus hirudinaceus

Description: Adults resemble *Ascaris suum*, but taper posteriorly. The anterior of the worm possesses a retractable proboscis, which is covered with recurved hooks (Fig. 1.87). Male worms are up to 10 cm long and the females around 40–60 cm in length and are slightly curved and white/pinkish in colour when fresh. The worms are thick (5–10 mm in width) and flattened and the cuticle is transversely wrinkled. This pseudo-segmentation can sometimes cause misidentification as a tapeworm. There is no alimentary canal. The anterior of the worm possesses a small retractable proboscis, which is covered with about six transverse rows of recurved hooks. The size of the hooks decreases posteriorly. The larva has a small circle of minute hooks at the anterior. The eggs are ovoid, yellowish-brown in colour, with a thick shell, the outer layer of which is irregularly mamillated (see Fig. 4.6) and measure 50–75 by 40–55 µm.

Life cycle: The prepatent period is 2–3 months and longevity can be around one year.

Oncicola

The main species is *Oncicola canis* which infects the small intestine of dogs, coyotes and occasionally cats. This parasite has beetles as intermediate hosts.

Oncicola canis

Description: These are thick worms (around 2–4 mm in width). Males are 6–13 mm and females 7–14 mm in length. The body is conical, tapering backwards, and is dark grey in colour. The proboscis bears six transverse rows, each with six hooks. The shapes of the hooks are taenioid in the anterior region and more like a rose thorn in the posterior section.

FAMILY POLYMORPHIDAE

A few genera are parasites of rodents (*Moniliformis*), aquatic birds (*Polymorphus*, *Filicollis*) and fishes (*Echinorhynchus*, *Acanthocephalus*). These are frequently small worms with a cylindrical body, although *Moniliformis* species can be very large, up to 30 cm in length.

Life cycle: The definitive host is infected following ingestion of an intermediate host that contains an infective cystacanth. The adult worm establishes in the posterior small intestine. The prepatent period is 3–4 weeks.

Polymorphus

The main species is *Polymorphus boschadis* (syn. *Polymorphus minutus*, *Echinorhynchus polymorphus*) which infects the small intestine of ducks, geese, chickens, swans and various wild aquatic birds. This parasite has crustaceans, including *Gammarus pulex*, freshwater shrimp and sometimes the crayfish *Potamobius astacus*, as intermediate hosts.

Polymorphus boschadis

Synonyms: *Polymorphus minutus*, *Echinorhynchus polymorphus*

Description: Males measure around 3 mm and females up to 10 mm in length and are orange-coloured when fresh. The anterior region possesses small spines and the cylindrical body has a constriction along its length, about one-third from the head. The proboscis has 16 rows of small hooks, their size increasing anteriorly. The spindle-shaped eggs have a thick middle shell, which is irregularly constricted towards the poles, and a thin outer shell, the embryo being slightly orange in colour. Eggs measure around 110 by 20 µm.

Filicollis

The main species is *Filicollis anatis* which infects the small intestine of ducks, geese, swans and various wild aquatic birds. This parasite has crustaceans, isopods such as *Asellus aquaticus*, as intermediate hosts.

Filicollis anatis

Description: The whitish male is about 7 mm in length and the anterior region possesses many small spines. The ovoid proboscis is armed with 18 longitudinal rows of small hooks. The neck of the female worm is elongate, slender and bears a globular-shaped proboscis, the crown of which is armed with 18 rows of minute hooks in a star-shaped pattern. The oval eggs measure approximately 62–67 by 19–23 µm. The eggs are smaller than those of *Polymorphus* and are oval rather than spindle-shaped.

PHYLUM PLATYHELMINTHES

This phylum contains the two classes of parasitic flatworms, the **Trematoda** and the **Cestoda**. A third class, the **Turbellaria** (planarians), which are mainly free-living carnivorous flatworms, are of no veterinary significance.

CLASS TREMATODA

Parasites of the class Trematoda (commonly called 'Flukes') include species of veterinary importance, which occur primarily in the bile ducts, alimentary tract and vascular system. Most flukes are flattened dorsoventrally, have a blind alimentary tract, suckers for attachment and are hermaphrodite (except Schistosomatidae where the sexes are separate). Depending on the predilection site, the eggs pass out of the final host, usually in faeces or urine, and the larval stages develop in a molluscan intermediate host. For a few species, a second intermediate host is involved, but the mollusc is essential for all members of the group.

There are many families in this class, and those which contain parasites of major veterinary importance include the Fasciolidae, Dicrocoeliidae, Paramphistomatidae and Schistosomatidae. Of lesser importance are the Echinostomatidae, Gastrodiscidae, Cyclocoelidae, Opisthorchiidae, Brachylaemidae, Heterophyidae, Diplostomatidae, Strigeidae and Lecithodendriidae. The most important family by far is the Fasciolidae and our discussion of structure, function and life cycle is largely oriented towards this group.

STRUCTURE AND FUNCTION OF TREMATODES

The adult is usually flat and leaf-like and possesses two muscular suckers for attachment. The oral sucker at the anterior end surrounds the mouth and the ventral sucker (called the acetabulum), as the name indicates, is on that surface. The body surface is a tegument, which is absorptive and is often covered with spines or scales. The muscles lie immediately below the tegument. There is no body cavity and the organs are packed in a parenchyma (Fig. 1.88).

The digestive system is simple, the oral opening leading into a pharynx, oesophagus and a pair of branched intestinal caeca, which end blindly. Undigested material is presumably regurgitated as flukes lack an anus. The excretory system consists of a large number of ciliated flame cells, which impel waste metabolic products along a system of tubules that ultimately join and open to the exterior, or to an excretory bladder. The nervous system is simple, consisting of a pair of longitudinal trunks connecting anteriorly with two ganglia.

The trematodes are usually hermaphrodite and both cross- and self-fertilisation may occur. The male reproductive system consists of a pair of testes, simple or branched, each leading into a vas deferens; these join to enter the cirrus sac containing a seminal vesicle and the cirrus, a primitive penis which terminates at the common genital opening (Fig. 1.88). In some flukes there is a cirrus sac surrounding these terminal organs. The female system has a single ovary leading into an oviduct (where eggs are fertilised), which is expanded distally to form the ootype. There the ovum acquires a yolk from the secretion of the vitelline glands and ultimately a shell. As the egg passes along the uterus, the shell becomes hardened and toughened and is finally extruded through the genital opening adjacent to the ventral sucker. The mature egg is usually yellow because of the tanned protein shell and most species have an operculum. The eggs of many species of fluke develop in the uterus and are therefore able to hatch once they are expelled. Food, generally blood or tissue debris, is ingested and passed into the caeca where it is digested and absorbed. Metabolism appears to be primarily anaerobic.

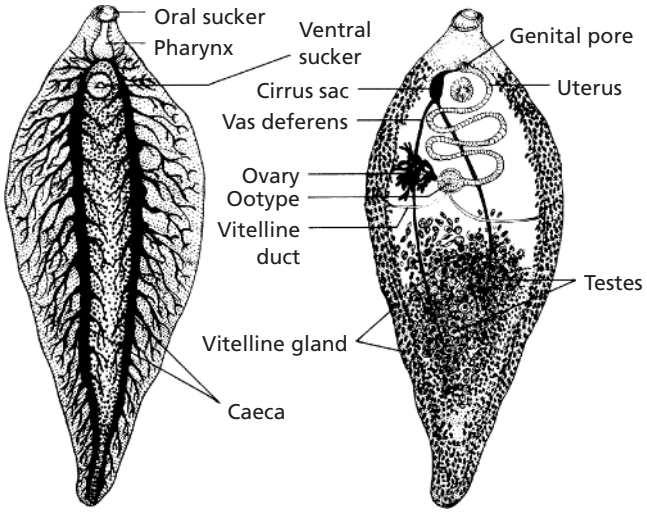


Fig. 1.88 Internal structure of a generalised digenetic trematode.

LIFE CYCLE OF TREMATODES

There is wide variation in the complex digenean life cycle. In general, the life cycle may have two or more obligate hosts, sometimes with transport or paratenic hosts. In most species, the first intermediate host is a mollusc in which futher development of hatched larvae takes place. The essential point of the life cycle is that whereas one nematode egg can develop into only one adult, one trematode egg may eventually develop into hundreds of adults. This is due to the phenomenon of asexual multiplication, **parthenogony**, in the molluscan intermediate host, i.e. the production of new individuals by single larval forms.

The adult flukes are always oviparous and lay eggs with an operculum or lid at one pole. In the egg, the embryo develops into a pyriform (pear-shaped) ciliated larva called a **miracidium** (Fig. 1.89). The eggs of some digenean flukes may be passively eaten by snails, in which they hatch. In many species of digenean flukes (e.g. *Fasciola hepatica*), the egg hatches in water and under the stimulus of light and temperature, the miracidium releases an enzyme that attacks the proteinaceous cement holding the operculum in place. The latter springs open like a hinged lid and the miracidium emerges within a few minutes.

The miracidium, propelled through the water by its cilia, does not feed and must, for its further development, find a suitable snail within a few hours before it exhausts its energy reserves. It is believed to use chemotactic responses to 'home in' on the snail and, on contact, it adheres by suction to the snail and penetrates its soft tissues using its conical papilla and aided by a cytolytic enzyme. The entire process of penetration takes about 30 minutes, after which the cilia are lost and the miracidium develops into an elongated sac, the **sporocyst**, containing a number of undifferentiated germinal cells. These cells develop into **rediae**, which migrate to the hepatopancreas of the snail; rediae are also larval forms possessing an oral sucker, some flame cells and a simple gut. From the germinal cells of the rediae arise the final stages, the **cercariae** (Fig. 1.90), although if environmental conditions for the snail are unsuitable, a second or daughter generation of rediae is often produced instead.

The cercariae, in essence young flukes with long tails, emerge actively from the snail, usually in considerable numbers. The actual stimulus for emergence depends on the species but is most commonly a change in temperature or light intensity. Once a snail is infected, cercariae continue to be produced indefinitely, although

Fig. 1.89 Miracidium of *Fasciola hepatica*.

Fig. 1.90 Cercaria of *Fasciola hepatica*.

the majority of infected snails die prematurely from gross destruction of the hepato-pancreas.

Typically, the cercariae swim for some time, utilising a film of water, and within an hour or so attach themselves to vegetation, shed their tails and encyst. This stage is called a **metacercaria** (Fig. 1.91), which is the infective stage for grazing animals. Encysted metacercariae have great potential for survival extending to months. Once ingested, the outer cyst wall is removed mechanically during mastication. Rupture of the inner cyst occurs in the intestine and depends on a hatching mechanism, enzymatic in origin, triggered by a suitable oxidation–reduction potential and a carbon dioxide system provided by the intestinal environment. The emergent juvenile fluke, often called a marita, then penetrates the intestine and migrates to the predilection site where it becomes adult after several weeks and starts to lay eggs, thus completing the cycle.

The location of the metacercariae varies between different flukes but in general they have a pattern. Those from fasciolids and paramphistomatids encyst on herbage. The metacercariae from troglotrematids, opisthorchiids and heterophyids encyst in fish, crab or crayfish intermediate hosts, whereas those from diplostomatids prefer amphibian or other vertebrate paratenic hosts. Schistosomatids do not have a metacercarial stage; the cercariae are able to penetrate the definitive host percutaneously.

Fig. 1.91 Metacercariae of *Fasciola hepatica*.

ORDER PLAGIORCHIIDA

FAMILY FASCIOLIDAE

These are large, flat leaf-shaped flukes. The anterior end is usually elongated into the shape of a cone and the anterior sucker is located at the end of the cone. The ventral sucker is placed at the level of the 'shoulders' of the fluke. The internal organs are branched while the cuticle is covered in spines. There are three important genera: *Fasciola*, *Fascioloides* and *Fasciolopsis*.

Fasciola

The members of this genus are commonly known as Liver flukes. They are responsible for widespread morbidity and mortality in sheep and cattle. The two most important species are *Fasciola hepatica* and *F. gigantica*. *F. hepatica* is found in the liver of sheep, cattle, goats, horses, deer, rabbits, humans and other mammals of temperate areas and in cooler areas of high altitude in the tropics and subtropics. *F. gigantica* predominates in tropical areas and is localised in the liver of cattle, buffalo, sheep, goats, pigs, camels, deer and humans (Fig. 1.92). Both species have lymnaeid snails as intermediate hosts.

Fasciola hepatica

Description: The young fluke at the time of entry into the liver is 1–2 mm in length and lancet-like (Fig. 1.92a). Adult flukes are leaf-shaped (being broader anteriorly than posteriorly), grey-brown in colour and around 2.5–3.5 cm in length and 1 cm in width (Fig. 1.93). The anterior end is conical and marked off by distinct shoulders from the body. The tegument is covered with backwardly

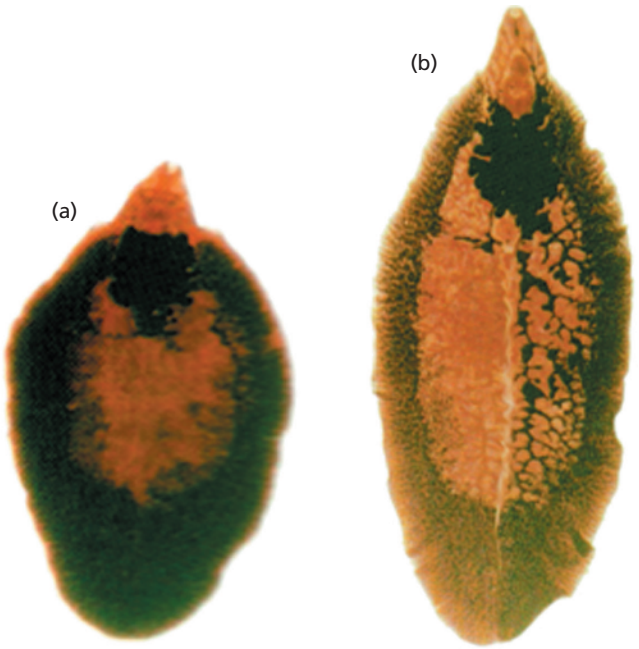


Fig. 1.92 Outline of (a) *Fasciola hepatica* and (b) *F. gigantica*. The former has broader shoulders and is shorter in length.

Fig. 1.93 Adult *Fasciola hepatica* fluke. (Courtesy of Jana Bulantova).

projecting spines. An oral and ventral sucker, situated at the level of the shoulders, may be readily seen. The intestinal caeca have many branches and extend a considerable distance posteriorly. The testes and ovary are multibranched. The uterus is positioned anterior to the testes. The cirrus is well developed. Immature flukes at the time of entry into the liver are 1–2 mm in length and lancet-like. The egg is thin-shelled, oval with symmetrical barrel-shaped side walls, operculate, browny-yellow and large (130–150 × 65–90 µm), and about twice the size of a trichostrongyle egg (Fig. 1.94; see also Fig. 4.3). The granular contents fill the whole of the egg.

Life cycle: Adult flukes in the bile ducts shed eggs into the bile and these enter the intestine. Eggs passed in the faeces of the mammalian host develop and hatch, releasing motile ciliated miracidia. This takes 9–10 days at optimal temperatures of 22–26 °C and little development occurs below 10 °C. The liberated miracidium has a short lifespan and must locate a suitable snail within about three hours if successful penetration of the latter is to occur. In infected snails, development proceeds through the sporocyst and redial stages to the final stage in the intermediate host, the cercaria; these are shed from the snail as motile forms, which attach themselves to firm surfaces, such as grass blades, and encyst there to form the infective metacercariae. It takes a minimum of 6–7 weeks for completion of development from miracidium to metacercaria, although under unfavourable circumstances a period of several months is required.

Infection of a snail with one miracidium can produce over 600 metacercariae. Metacercariae ingested by the final host excyst in the small intestine, migrate through the gut wall, cross the peritoneum and penetrate the liver capsule. The young flukes tunnel through the liver parenchyma for 6–8 weeks and then enter the small bile ducts where they migrate to the larger ducts and occasionally the gallbladder and reach sexual maturity. The prepatent period is 10–12 weeks. The minimal period for completion of one entire life cycle of *F. hepatica* is therefore 17–18 weeks. The longevity of *F. hepatica* in untreated sheep may be years; in cattle it is usually less than one year. See **life cycle 18**.

Fasciola gigantica

Description: The adult fluke is larger than *F. hepatica*, reaching 7.5 cm in length and 1.5 cm in breadth, and the body is more transparent. The shape is more leaf-like, the conical anterior end is very short and the shoulders, characteristic of *F. hepatica*, are barely perceptible (Fig. 1.92b). The gut caeca are more highly branched than in *F. hepatica*. The eggs are larger than those of *F. hepatica*, measuring 170–190 by 90–100 µm.

Life cycle: This is similar to *F. hepatica*, the main differences being in the time scale of the cycle. The immature stages migrate through the liver parenchyma, the adults reaching the bile ducts about 12 weeks after infection. Most parasitic phases are longer and the prepatent period is 13–16 weeks.

Fascioloides

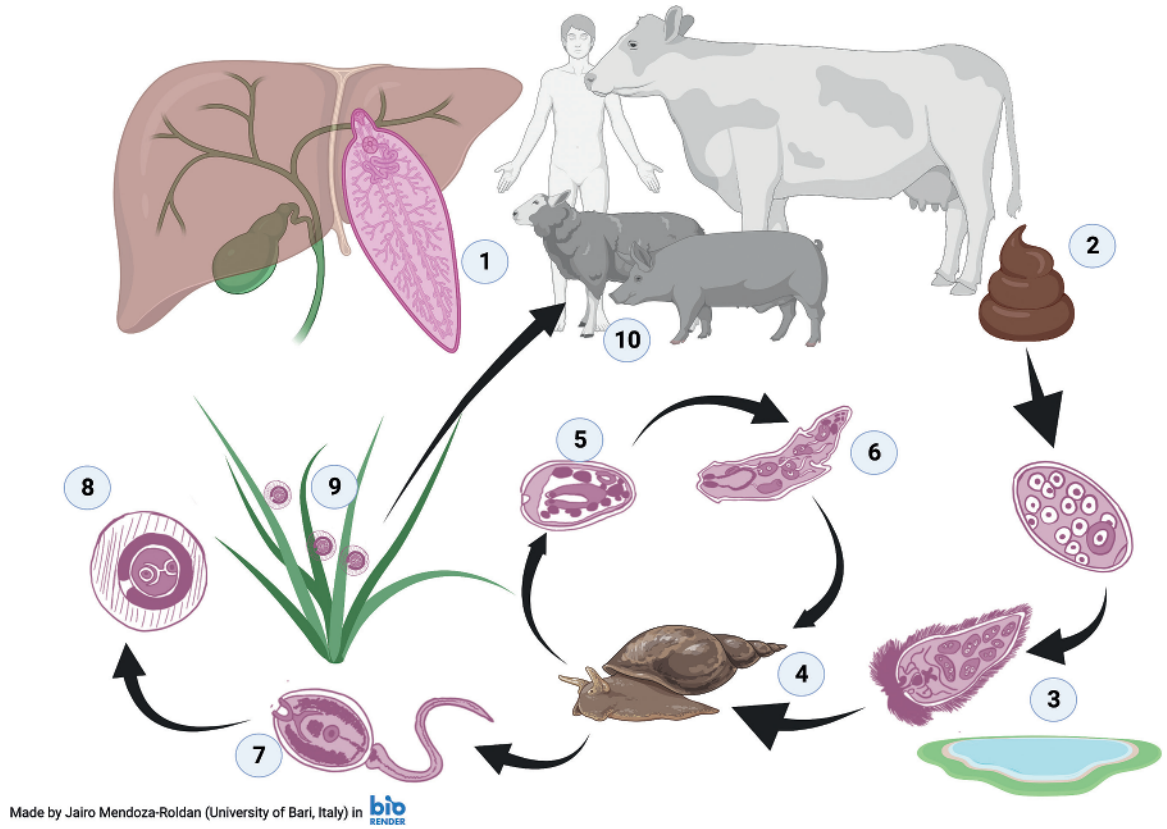
The genus comprises a single species, *Fascioloides magna*, also known as the giant liver fluke, large American liver fluke or deer fluke. It is one of the largest of the trematodes and is easily identified.

Life cycle: The life cycle is similar to that of *F. hepatica*. The eggs hatch to miracidia after four weeks or longer. Development in the snail takes 7–8 weeks. The prepatent period in deer is around 30 weeks. The main species is *Fascioloides magna* which infects the liver and occasionally bile duct of deer, cattle, sheep, goats, pigs, horses and llamas. This parasite has lymnaeid snails (*Fossaria* spp., *Lymnaea* spp., *Stagnicola* spp.) as intermediate hosts.

Fig. 1.94 Rumen fluke eggs (Paramphistomatidae) with yellow-brown egg of *Fasciola hepatica* (left). (Courtesy of Anja Joachim).

LIFE CYCLE 18. LIFE CYCLE OF *FASCIOLA HEPATICA*

Fasciola hepatica is a trematode parasite of the biliary ducts (1) of small and large ruminants, which excrete the parasite eggs with the faeces (2). Upon contact with water, miracidia (larvae with vibrating cilia, 3) hatch from the egg and actively swim to seek out a suitable intermediate host, freshwater snails of the family Lymnaeidae (4). The miracidium enters the foot of the snail and travels to the hepatopancreas where it develops into a sporocyst (5). Subsequently, the sporocyst generates rediae (6), that localise in the respiratory tract, and then several cercariae (7). The latter stage is highly motile, and actively leaves the intermediate host to become encysted as metacercaria (8) on aquatic plants, such as watercress (9). Once ingested by suitable definitive hosts (including humans) (10), the metacercaria hatches and begins migrating as a juvenile form (adolescaria) from the intestine through the peritoneum to the parenchyma of the liver and finally to the biliary ducts, where it develops into a sexually mature adult trematode.



Fascioloides magna

Description: Flukes are large and thick and measure up to 10 cm long by 2.5 cm broad and around 3–4 mm in depth. The flukes are oval, with a rounded posterior end. They possess no anterior cone projection and when fresh are flesh-coloured (Fig. 1.95). In deer, adult *F. magna* occur in cysts which communicate with the bile ducts. Eggs are large, operculate, measure 109–168 by 75–96 µm and have a protoplasmic appendage at the pole opposite the operculum.

Fasciolopsis

The single species of this genus is primarily a parasite of humans in India, Pakistan, Southeast Asia and China, but can occur in the pig which may act as a reservoir host.

Life cycle: The life cycle is similar to that of *F. hepatica*. The final host is infected through ingestion of metacercariae that encyst on aquatic plants. The prepatent period is 9–13 weeks. The main species is *Fasciolopsis buski* which infects the small intestine of humans, pigs and occasionally dogs. This parasite has freshwater snails (*Planorbis*, *Segmentina*, *Hippeutis*) as intermediate hosts.

Fasciolopsis buski

Description: Large, thick, elongate–oval, fleshy pink flukes without shoulders, broader posteriorly, and variable in size but usually measuring 30–75 mm long by 8–20 mm wide. The ventral sucker is located near the anterior extremity and is much larger than the oral sucker. The cuticle is covered in spines that are frequently lost as adults. The intestinal caeca are unbranched and extend to near the posterior of the fluke. The testes are branched and tandem; the ovary is also branched. Eggs are oval, yellowish-brown, thin-shelled with an operculum, and measure 125–140 by 70–90 µm (Fig. 1.96). They resemble those of *Fasciola*.

Fig. 1.95 *Fascioloides magna*.

Fig. 1.96 Egg of *Fasciolopsis buski*.

FAMILY PARAMPHISTOMATIDAE

Adult paramphistomes (amphistomes) are mainly parasitic in the forestomachs of ruminants, although *Gigantocotyle* is found in the liver and duodenum. Their shape is not typical of the trematodes, being conical and thick and fleshy rather than flat. All require a water snail as an intermediate host. There are several genera: *Paramphistomum*, *Cotylophoron*, *Bothriophoron*, *Orthocoelium* and *Gigantocotyle*, of which *Paramphistomum* is the most common and widespread in ruminants. The taxonomy of the paramphistomes is complex and unresolved and many of the species described may be synonymous, being differentiated mainly on size and shape of the suckers.

Paramphistomum

Members of this genus (rumen fluke) are found in the rumen and reticulum of ruminants (Table 1.49). The adults are small, conical (pear-shaped), maggot-like flukes about 1 cm long and 3–5 mm wide and light red in colour when fresh. Unlike other flukes, the large ventral sucker is located at the posterior extremity of the body and is well developed.

Life cycle: Eggs shed in the faeces are undeveloped. In an aquatic environment, miracidia develop and hatch to penetrate water snails in which they develop to cercaria, following sporocyst and redial stages. The cercariae encyst (metacercariae) on vegetation in, or bordering, watercourses and ponds. Development in the snail intermediate host is similar to that of *Fasciola* and under favourable conditions (26–30 °C) can be completed in four weeks. Following ingestion by a definitive host, the metacercariae excyst in the duodenum, where the young flukes attach and feed for about six weeks, before migrating forward to the forestomachs where they mature. The prepatent period is between seven and 10 weeks.

Paramphistomum cervi

Synonym: *Paramphistomum explanatum*

Description: Adult flukes measure about 6–13 mm by 3–5 mm. The adults are small, conical (pear-shaped), maggot-like flukes

Table 1.49 *Paramphistomum* (*Calicophoron*, *Cotylophoron*, *Bothriophoron*) species.

Species	Hosts	Site	Intermediate hosts
Paramphistomum cervi (syn. *Paramphistomum explanatum*)	Cattle, sheep, goats, deer, buffalo, antelopes	Rumen	Freshwater snails (*Bulinus* spp., *Planorbis* spp.)
Calicophoron daubneyi (syn. *Paramphistomum daubnei*, *Paramphistomum daubneyi*)	Cattle, goats	Rumen	Freshwater snails (*Omphiscola* spp.)
Paramphistomum microbothrium	Cattle, sheep, goats, deer, buffalo, antelopes	Rumen	Freshwater snails (*Fossaria* spp., *Bulinus* spp.)
Paramphistomum ichikawa	Sheep, cattle	Rumen	Planorbid snails (*Gyraulus*, *Helicorbis*, *Segnetilia*)
Cotylophoron cotylophorum (syn. *Paramphistomum cotylophorum*)	Sheep, goats, cattle and wild ruminants	Rumen, reticulum	Freshwater snails (*Bulinus* spp.)
Paramphistomum bothriophoron (syn. *Bothriophoron bothriophoron*)	Zebus	Rumen	Freshwater snails (*Bulinus* spp., *Planorbis* spp.)
Paramphistomum streptocoelium (syn. *Ceylonocotyle streptocoelium*, *Orthocoelium streptocoelium*)	Cattle, sheep, goats and wild ruminants	Rumen	Freshwater snails (*Glyptanisus* spp.)
Calicophoron calicophorum (syn. *Paramphistomum calicophorum*)	Cattle, sheep, other ruminants	Rumen, reticulum	Water snails

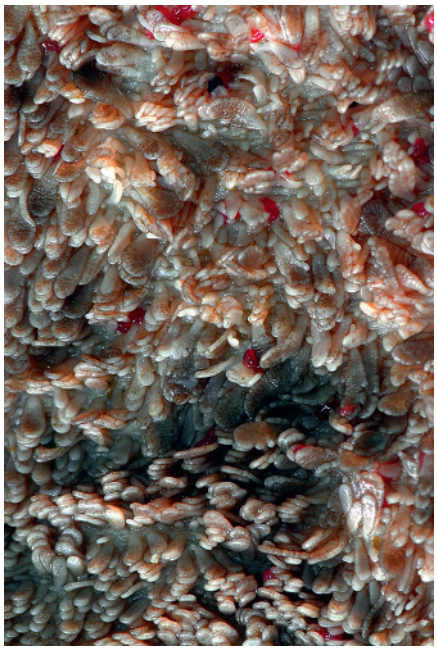


Fig. 1.97 Adult flukes of *Paramphistomum*. (Courtesy of Andrei Mihalca).

about 1 cm long and light red in colour when fresh (Fig. 1.97). One sucker is visible at the tip of the cone and the other well-developed sucker is at the base. The tegument has no spines. The larval stages are less than 5 mm, fresh specimens having a pink colour. The egg resembles that of *Fasciola hepatica*, being large (about 115–175 by 75–100 µm) and operculate, but is transparent or slightly greenish rather than yellowish-brown and slightly smaller than eggs of *F. hepatica* (see Fig. 1.94). In the early stages of segmentation, the egg contains 4–8 blastomeres surrounded by yolk cells.

Cotylophoron cotylophorum

Synonym: *Paramphistomum cotylophoron*

Description: The fluke is very similar to *Paramphistomum cervi* but the genital pore is surrounded by a genital sucker. The egg measures 125–135 by 60–68 µm.

Gigantocotyle

Gigantoctyle is found in the liver and duodenum of cattle and other ruminants. The life cycle is similar to that of *F. hepatica* and requires snails of the genus *Galba* as intermediate hosts. The main species is *Gigantocotyle explanatum* (syn. *Explanatum explanatum*, *Paramphistomum explanatum*) which infects the liver, bile ducts, gallbladder and duodenum of cattle, buffalo and other ruminants. This parasite has freshwater snails as intermediate hosts.

Gigantocotyle explanatum

Synonyms: *Paramphistomum explanatum*, *Paramphistomum fraturnum*, *Explanatum explanatum*

Description: These are conical pinkish flukes when fresh. Adult fluke are 8–10 mm long and 4.7–5.7 mm wide. The body tapers anteriorly and is curved ventrally with no tegumental papillae. The acetabulum is very large and the genital pore is bifurcal. The oval eggs measure 180–200 by 110–130 µm, are colourless and have an operculum.

Pseudodiscus

Adult flukes have a conical anterior end widening gradually to an oval leaf-like shape. The main species is *Pseudodiscus collinsi* which infects the caecum and colon of horses. This parasite has freshwater snails (*Indoplanorbis* spp.) as intermediate hosts.

Pseudodiscus collinsi

Description: Adult flukes are 6–12 mm by 3–7 mm in size. The conical body has conspicuous serrations along the anterior lateral margins. There is a ventral sucker and the oral sucker has paired pouch-like diverticula.

FAMILY GASTRODISCIDAE

Gastrodiscus spp. are found in the large intestines of horses and pigs. *Homalogaster* is found in the large intestine of cattle and buffalo.

Gastrodiscus

Intestinal flukes with a short conical anterior end and a large posterior discoid body covered ventrally with large papillae (Table 1.50).

Life cycle: The life cycle of the different species is generally similar. Eggs are passed in the faeces and, following development, release miracidia into water where they enter a species of water snail. Development in the snail proceeds through sporocyst and redial stages leading to the release of cercariae, which encyst to form metacercariae. Infection of the final host is by ingestion of metacercariae with herbage. Excystation occurs in the intestine where the immature paramphistomes develop to reach maturity.

Gastrodiscus aegyptiacus

Description: Adult flukes are reddish-pink in colour when fresh and measure 9–17 mm by 8–11 mm. The anterior region measures up to 4 mm by 2.5 mm and is cylindrical, while the remainder of the body is saucer-shaped, with the margins curved inwards (Fig. 1.98). The ventral surface is covered by a large number of regularly arranged papillae. The oral sucker has two posterolateral pouches;

Table 1.50 *Gastrodiscus* species.

Species	Hosts	Site	Intermediate hosts
Gastrodiscus aegyptiacus	Horses, donkeys, pigs, warthogs	Large and small intestine	Freshwater snails (*Bulinus* spp., *Cleopatra* spp.)
Gastrodiscus hominis (syn. *Gastrodiscoides hominis*)	Pigs, humans	Caecum, colon	Planorbid snails (*Helicorbis* spp.)
Gastrodiscus secundus	Horses, elephants	Large intestine	Freshwater snails (*Bulinus* spp.)

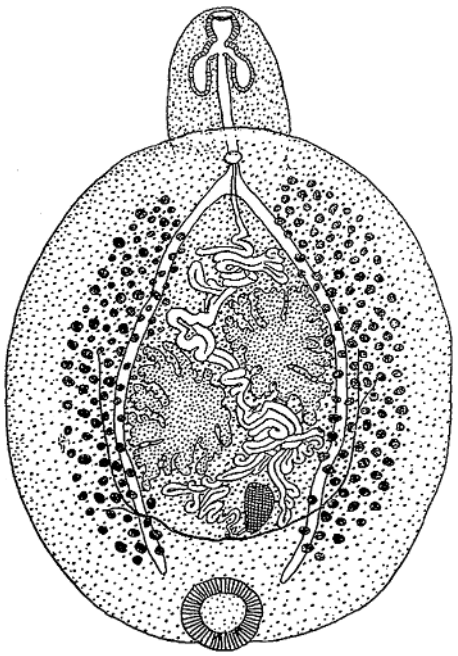


Fig. 1.98 *Gastrodiscus aegyptiacus.* (Adapted from Mönnig, 1934).

the posterior sucker is small and subterminal. Eggs are oval and measure 131–139 by 78–90 µm.

Gastrodiscus hominis

Synonym: *Gastrodiscoides hominis*

Description: Adult flukes are pink in colour when fresh and measure 8–14 mm by 5–8 mm, with a conical anterior body and a large discoidal posterior body lacking tegumental papillae.

Gastrodiscus secundus

Description: Identical to *G. aegyptiacus* but the genital pore is located posterior to the level of the caecal origin and the vitelline glands are distributed all over the discoid posterior body.

Homalogaster

These are intestinal flukes in which the body is divided into two, with a large anterior region and a small cylindrical posterior region.

Life cycle: The life cycle is presumed to be similar to other paramphistomes of the rumen. The main species is *Homalogaster paloniae* which infects the large intestine of cattle and buffalo. This parasite has freshwater snails (*Hippeutis* spp., *Polypylis* spp.) as intermediate hosts.

Homalogaster paloniae

Description: Adult flukes are 8–15 mm long and 4.5–7.5 mm wide. The anterior body is large, flat, ellipsoidal and bluntly pointed anteriorly with large numbers of papillae present on the ventral tegument. The posterior body is small and spherical.

FAMILY GASTROTHYLACIDAE

Pouched amphistomes are similar in appearance to the paramphistomes, with a number of species belonging to the genera *Gastrothylax*, *Fischoederius* and *Carmyerius* parasitic in ruminants throughout Africa and Asia. These flukes differ in having an extremely large ventral pouch that opens anteriorly and which covers the ventral surface of the fluke as far as the large ventral sucker.

Gastrothylax

The main species is *Gastrothylax crumenifer* which infects the rumen and reticulum of cattle, buffalo, zebu, sheep and other ruminants. This parasite has freshwater snails as intermediate hosts.

Gastrothylax crumenifer

Description: This is an elongated fluke, being circular in transverse section and reddish in colour when fresh. The body is 10–16 mm long and 5–8 mm wide. This fluke differs in having an extremely large ventral pouch that opens anteriorly and which covers the ventral surface of the fluke as far as the large ventral sucker. The ventral pouch is normally triangular in cross-section with a dorsally directed apex. The terminal genitalium opens into the ventral pouch about halfway between the intestinal bifurcation and the pharynx. The terminal oval sucker is small. Eggs are 115–135 by 66–70 µm.

Fischoederius

Fischoederius spp. complete their biological life cycle in freshwater snails, and are localised in the rumen and duodenum of cattle, buffalo, zebu, sheep and other ruminants. *Fischoederius elongatus* may rarely infect humans.

Fischoederius elongatus

Description: The flukes are reddish when fresh. The body is 10–20 mm long and 3–5 mm wide. The terminal genitalium is within the ventral pouch. The uterus is situated along the midline. The testes are lobed and one is sited dorsally to the other. Eggs measure 125–150 by 65–75 µm.

Fischoederius cobboldi

Description: The flukes are reddish in colour when fresh. The body measures 8–10 mm in length. Eggs measure 110–120 by 60–75 µm.

Carmyerius

Carmyerius spp. complete their biological life cycle in freshwater snails, and are localised in the rumen of cattle, buffalo and antelopes.

Carmyerius spatiosus

Synonym: *Gastrothylax spatiosus*

Description: Flukes measure 8.5–12 mm in length and 2.5–3 mm in width. The posterior sucker is quite small and is spherical. The intestinal caeca extend down into the last quarter of the body. The ventral pouch is either circular or slightly triangular with blunt angles and the terminal genitalium lies within the pouch. The testes lie horizontally, one on each side of the median line, which differs from the position in *Fischoederius*. Eggs measure 115–125 by 60–65 µm.

Carmyerius gregarius

Description: The flukes are 7–10 mm in length. The intestinal caeca extend only a short distance below the middle of the body.

FAMILY ECHINOSTOMATIDAE

The family Echinostomatidae includes the genera *Echinostoma*, *Echinoparyphium* and *Hypoderaeum*, which are parasites of birds, and *Echinochasmus*, *Isthmiophora* and *Euparyphium*, which are parasites of fish-eating mammals.

Life cycle: The life cycle involves two intermediate hosts, namely freshwater snails and fish or frogs. Eggs passed in the faeces of infected birds hatch to produce a miracidium, which infects the first intermediate snail host. Subsequently, cercariae encyst within the snail or are shed and migrate to infect other snails. Cercariae can also encyst in the kidneys of tadpoles and adult frogs. The definitive host is infected through eating the second intermediate host containing encysted metacercariae (mesocercariae). The prepatent period is 1–2 weeks.

Echinostoma

Echinostoma revolutum are localised in the rumen, caecum, cloaca and rectum of ducks, geese, fowl, partridges and pigeons (*Echinostoma revolutum*), and occasionally humans. *Echinostoma paraulum* are localised in the small intestine of ducks, pigeons and humans. Both species complete their biological life cycle in snails and frogs.

Echinostoma revolutum

Description: The fluke is about 10–20 mm long and up to 2 mm in width. The head-collar is armed with around 37 spines, some forming groups of 'corner' spines. The anterior of the cuticle is covered in spines. The ovary is anterior to the tandem testes.

Echinostoma paraulum

Synonym: *Echinoparyphium paraulum*

Description: The fluke measures 6–10.5 mm in length by 0.8–1.5 mm in width. The tegument is usually almost completely covered in spines, but in some instances these can be absent. The head-collar is armed with 37 spines, some forming a double dorsolateral row. The tandem testes are located in the third quarter of the body.

Echinoparyphium

The main species is *Echinoparyphium recurvatum* which infects the small intestine of ducks, geese, chickens, pigeons, wild birds and humans. This parasite has snails, fish, shellfish and tadpoles as intermediate hosts.

Echinoparyphium recurvatum

Description: The fluke is about 4 mm long by 0.7 mm wide and curved ventrally. Spines are present anterior to the ventral sucker and the head-crown is armed with spines. Eggs measure about 110 by 82 µm.

Hypoderaeum

The main species is *Hypoderaeum conoideum* which infects the small intestine of chickens, turkey, ducks, geese, pigeons and other aquatic birds. This parasite has snails, fish, shellfish and tadpoles as intermediate hosts.

Hypoderaeum conoideum

Description: Adult flukes have an elongate body 5–12 mm long and tapering posteriorly. The anterior body is armed with about 50 small spines and bears a large ventral sucker. The testes are elongate and slightly lobed, and situated just beyond the midline.

Echinochasmus

The main species is *Echinochasmus perfoliatus* which infects the small intestine of dogs, cats, foxes and pigs. This parasite has snails and fish as intermediate hosts.

Echinochasmus perfoliatus

Description: Adult flukes are 2–4 mm long with a head-crown bearing 24 spines arranged in a single row. The testes are large and situated just beyond the midline, with the ovaries to the right and anterior to the testes.

Euparyphium

Euparyphium spp. complete their biological life cycle in snails and amphibian tadpoles, and are localised in the small intestine of cats, foxes, polecats, mink, badgers, otters, hedgehogs (*Euparyphium melis*), humans, dogs and rats (*Euparyphium ilocanum*).

Euparyphium melis

Description: Adult flukes have an elongate body 3.5–12 mm long that bears a large ventral sucker and a dorsal head-collar with 27 spines. The whole ventral surface is covered with small spines. The testes are situated midline, with one lying posterior to the other. The ovary lies anterior to the testes and to the right of the midline.

FAMILY PHILOPHTHALMIDAE

Philophthalmus are eye flukes of birds.

Life cycle: Embryonated eggs are shed from the eyes, mouth and nostrils, and hatch immediately on contact with water. After penetrating a snail intermediate host, a single redia is released. The mother redia penetrates the heart of the snail, releasing daughter rediae that migrate to the digestive glands and after about 95 days produce cercariae, which are released from the snail and encyst on aquatic vegetation. Following ingestion, metacercariae excyst in the mouth or crop and young flukes may be found in the oesophagus, nasal passages, orbit and lacrimal gland within a few hours following ingestion.

Philophthalmus

The main species is *Philophthalmus gralli* (the Oriental avian eye fluke) which infects the conjunctival sac of ostriches, chickens and wild birds. This parasite has freshwater snails as intermediate hosts.

Philophthalmus gralli

Description: Adult flukes are very small (2–3 mm) and fusiform shaped. The body surface is covered by small spines and the two suckers are orally and subterminally located. The pharynx is located immediately posterior to the oral sucker.

FAMILY CYCLOCOELIDAE

These are medium-sized to large slightly flattened flukes, parasites of aquatic birds in the body cavity, air sacs or nasal cavities. They do not possess an oral sucker and often the ventral sucker is absent. The intestinal caeca are joined together posteriorly and their structure is simple or branched. The lateral vitellaria similarly meet posteriorly. Genera include *Typhlocoelum* in the respiratory tract of ducks and *Hyptiasmus* in the nasal and orbital sinuses of ducks and geese.

Typhlocoelum

Life cycle: Eggs are coughed up and swallowed in the faeces of ducks. A miracidium, containing a single redia, hatches from the egg. The redia, not the miracidium, enters a snail and after 11 days produces small numbers of cercariae. There is no sporocyst stage. The cercariae are retained within the snail and encyst. Birds are infected by eating infected snails of the genera *Helisoma* and *Planorbis*. The larval fluke reaches the bronchi via the bloodstream.

Typhlocoelum cucumerinum

Synonyms: *Distoma cucumerinum*, *Typhloceolum obovlae*

Description: Adult flukes are 6–12 mm long by 2–5 mm broad. The body is oval and blunter anteriorly than posteriorly. The testes are deeply lobed and lie diagonally one behind the other with the unlobed ovary situated in front of the posterior testis.

Typhlocoelum cymbium

Synonym: *Tracheophilus sisowi*

Description: Adult flukes are 6–11.5 mm long by 3 mm broad. The body has rounded ends and is wide in the middle. The testes are rounded, not lobed, and lie in a diagonal position in the posterior part of the body with the unlobed ovary situated in front of the anterior testis. Eggs measure about 122 by 63 µm.

Hyptiasmus

The main species is *Hyptiasmus tumidus* (syn. *Hyptiasmus arcuatus*, *Cyclocoelum arcuatum*) and infects the nasal and orbital sinuses of ducks and geese. This parasite has water snails as intermediate hosts.

Hyptiasmus tumidus

Synonyms: *Hyptiasmus arcuatus*, *Cyclocoelum arcuatum*

Description: Adult flukes are 7–20 mm long by 2–5 mm wide. The body is pyriform and more rounded posteriorly. The gonads are arranged in a straight line.

FAMILY NOTOCOTYLIDAE

The family Notocotylidae includes the genera *Notocotylus*, *Paramonostomum* and *Catatropis*, which are parasites of birds, and *Cymbiforma*, which occur in sheep, goats and cattle. The small eggs are characterised by long filaments at the poles. The intermediate hosts are water snails.

Notocotylus

The main species is *Notocotylus attenuatus* which infects the caecum and rectum of chickens, ducks, geese and wild aquatic birds. This parasite has snails as intermediate hosts.

Notocotylus attenuatus

Description: The adult flukes are 2–5 mm long by 0.7–1.5 mm wide, narrow anteriorly and have no ventral sucker. The testes are situated posteriorly and the ovary lies between them. The uterus forms regular transverse coils extending from the posterior ovary to the elongate cirrus sac, situated anteriorly.

Catatropis

The main species is *Catatropis verrucosa* which infects the caeca of chickens, ducks, geese and other aquatic birds. This parasite has snails as intermediate hosts.

Catatropis verrucosa

Description: The fluke is 2–6 mm long and rounded anteriorly and posteriorly and has no ventral sucker. The testes are situated posteriorly and the ovary lies between them.

Cymbiforma

The main species is *Cymbiforma indica* (syn. *Ogmocotyle indica*) which infects the small intestine of sheep, goats and cattle. This parasite has snails as intermediate hosts.

Cymbiforma indica

Synonym: *Ogmocotyle indica*

Description: Adult flukes are pear-shaped, concave ventrally and measure 0.8–2.7 cm in length and 0.3–0.9 mm in width. There is no ventral sucker and the cuticle is armed with fine spines ventrally and anteriorly. The ovary has four demarcated lobes. The fluke lacks a pharynx and the oesophagus is short. The genital opening is sited just anterior to the middle of the body and to the left of the midline. Eggs bear long filaments at both poles and measure 18–27 by 11–13 µm.

FAMILY DICROCOELIIDAE

These trematodes are small lancet-like flukes occurring in the biliary and pancreatic ducts of vertebrates. Miracidia are present in the eggs when they are passed in the faeces; there is no redial stage during development in the snail and 2–3 intermediate hosts may be involved in the life cycle. Members of this family are found in ruminants (*Dicrocoelium*, *Eurytrema*), cats and birds (*Platynosomum*).

Dicrocoelium

The single species of this genus is found in the bile ducts of the liver of ruminants. There is no possibility of confusion with other flukes in the bile ducts of ruminants due to their small size and distinct lanceolate shape.

Life cycle: The egg does not hatch until ingested by the first intermediate host, a terrestrial snail, in which two generations of sporocysts develop which then produce cercariae. The latter are extruded in masses cemented together by slime and adhere to vegetation. This phase of development takes at least three months. The slime balls of cercariae are ingested by ants in which they develop to metacercariae, mainly in the body cavity and occasionally the brain. The presence of a brain lesion in the ant, induced by metacercariae, impels the ant to climb up and remain on the tips of the herbage, thus increasing the chance of ingestion by the final host. This phase in the ant is completed in just over one month in summer temperatures. Infection of the final host is by passive ingestion of ants containing metacercariae. The metacercariae hatch in the small intestine and the young flukes migrate up the main bile duct and thence to the smaller ducts in the liver. There is no parenchymal migration and the prepatent period is 10–12 weeks. The total life cycle takes approximately six months. The flukes are long-lived and can survive in the final host for several years. See **life cycle 19**.

Dicrocoelium dendriticum

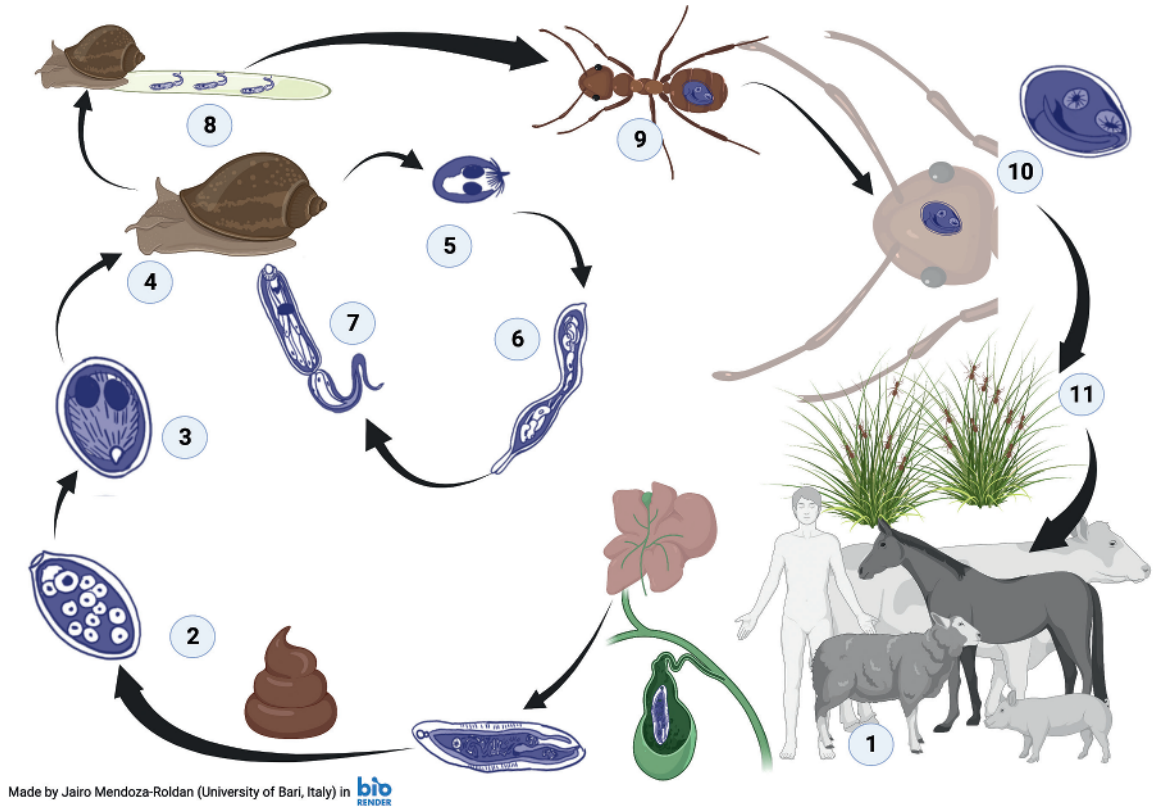
Synonym: *Dicrocoelium lanceolatum*

Description: Adult flukes are 6–12 mm long and 1.5–2.5 mm wide, distinctly lanceolate and semi-transparent/translucent allowing the internal organs to be readily seen (Fig. 1.99). They are almost symmetrical in shape and the cuticle is smooth. The oral sucker is smaller than the ventral sucker and is located in close proximity. The gut is simple, consisting of two branches resembling a tuning fork. Behind the ventral sucker, the lobed testes lie in tandem with the ovary immediately posterior. The uterus is usually dark brown and convoluted, filling the space behind the genital gland. The cirrus is small. There are no spines on the cuticle (cf. *Fasciola*). The thick-shelled egg is small, 35–45 µm in length by 22–30 µm in width, dark brown with small round poles and slightly barrel-shaped walls and operculate, usually with a flattened side. The operculum is often difficult to see. It contains a miracidium that completely fills the egg when passed in the faeces.

Fig. 1.99 *Dicrocoelium dendriticum*.

LIFE CYCLE 19. LIFE CYCLE OF *DICROCOELIUM DENDRITICUM*

Adult *Dicrocoelium dendriticum* live in the biliary ducts and gallbladder of cattle and other grazing animals, which are definitive hosts; humans can be accidental definitive hosts (1). These excrete parasite eggs with the faeces (2). In the environment, a miracidium develops inside the egg (3). Once eggs containing the miracidia are ingested by terrestrial gastropods (first intermediate hosts, 4), the miracidia hatch (5) and migrate to the snail hepatopancreas, where they form first- and second-generation sporocysts (6); these generate tailed cercariae (7) that leave the intermediate hosts via mucus secretions (slime balls, 8) and are ingested by the second intermediate hosts (9), i.e. ants (e.g. *Formica fusca* and *Formica rufibarbis*). Once ingested, the cercariae encyst in the body of the ant, thus becoming metacercariae (9), with one or two localising to the pharyngeal ganglion (10); during the cooler evening hours of the day, the latter enlarge, causing infected ants to undergo spastic paralysis (11). Thus, infected ants cling to the tips of grass blades, facilitating their ingestion by suitable definitive hosts. Once in the intestine of the definitive host, the metacercariae begin migrating to the liver via the common bile duct, and mature into adult trematodes within 70–85 days (1).



Dicrocoelium hospes

Description: Details are essentially similar to *D. dendriticum* and the flukes are usually found in the liver and gallbladder of cattle, oxen and occasionally sheep and goats in parts of Africa.

Eurytrema

This genus inhabits the pancreatic ducts and sometimes the bile ducts of ruminants (Table 1.51).

Eurytrema pancreaticum

Synonyms: *Distoma pancreaticum*, *Eurytrema ovis*

Description: Oval, leaf-shaped, reddish-brown flukes measuring around 8–16 mm long by 5–8.5 mm wide (Fig. 1.100). The body is thick and the juvenile flukes are armed with spines which are often absent by the adult stage. The oral sucker is larger than the ventral sucker and the pharynx and oesophagus are short. The testes are

Table 1.51 *Eurytrema* species.

Species	Hosts	Site	Intermediate hosts
Eurytrema pancreaticum (syn. *Distoma pancreaticum*, *Eurytrema ovis*)	Cattle, buffalo, sheep, goats, pigs, camels, humans, primates	Pancreas; rarely bile ducts Perirenal fat	Land snails, particularly of the genus *Bradybaena* Grasshoppers of the genus *Conocephalus* or tree crickets (*Oecanthus*)
Eurytrema coelomaticum (syn. *Distoma coelomaticum*)	Cattle, sheep	Pancreas; rarely bile ducts	Land snails, particularly of the genus *Bradybaena* Grasshoppers of the genus *Conocephalus* or tree crickets (*Oecanthus*)
Eurytrema procyonis	Cats, foxes, raccoons	Pancreas	Snails of the genus *Mesodon* Grasshoppers

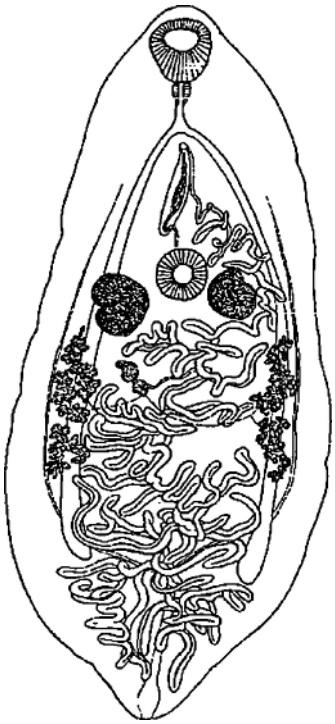


Fig. 1.100 *Eurytrema pancreaticum*. (Soulsby, 1971. Reproduced with permission from Lord Soulsby of Swaffham Prior.)

positioned horizontally just behind the ventral sucker. A tubular cirrus sac is present. The uterus completely occupies the posterior body. Eggs measure around 40–50 by 25–35 µm and are similar to those of *Dicrocoelium*.

Life cycle: Eggs passed in faeces are ingested by a snail where two generations of sporocysts occur. Cercariae are released onto the herbage about five months after initial infection and these are ingested by grasshoppers. Infective metacercariae are produced in about three weeks. The final host becomes infected by accidentally eating the second intermediate host. Metacercariae encyst in the duodenum and migrate to the pancreas via the pancreatic duct and reside in the small ducts of the pancreas. The prepatent period in cattle is 3–4 months.

Eurytrema coelomaticum

Synonym: *Distoma coelomaticum*

Description: A leaf-shaped reddish brown fluke with adults measuring around 8–12 by 6–7 mm.

Eurytrema procyonis

Description: The adult measures about 2.9 mm long by 1.2 mm wide. The oral sucker is subterminal with a dorsal lip-like projection. The eggs are small, 45 by 35 µm, asymmetrical, dark brown with an operculum and a miracidium.

Life cycle: The life cycle is unknown but is thought to involve snail intermediate hosts of the genus *Mesodon*. Animals are likely to become infected by ingestion of the snail intermediate host.

Table 1.52 *Platynosomum* species.

Species	Hosts	Site	Intermediate hosts
Platynosomum fastosum (syn. *Eurytrema fastosum*)	Cats	Bile and pancreatic ducts	Land snails (*Sublima*) and woodlice Lizards are obligate paratenic hosts
Platynosomum concinnum	Cats	Bile and pancreatic ducts	Land snails (*Sublima*) and woodlice Lizards are obligate paratenic hosts
Platynosomum illiciens	Cats	Bile and pancreatic ducts	Land snails (*Sublima*) and woodlice Lizards are obligate paratenic hosts

Platynosomum

Flukes of this genus are found in wild birds, but some species are also found in the liver of cats (Table 1.52).

Platynosomum fastosum

Description: The adult fluke is lanceolate and measures 4–8 mm by 1.5–2.5 mm in size. The testes lie obliquely horizontal. The eggs are brown, oval, thick-shelled and operculate and measure about 34–50 by 23–35 µm. They are embryonated when laid.

Life cycle: Eggs passed in the faeces develop in a land snail (*Sublima*) and a crustacean (woodlouse). Cercariae encyst when a lizard, gecko, skink or toad eats the woodlouse. The cat is infected by ingesting a lizard or other host containing metacercariae, which acts as an obligate paratenic host. The prepatent period is around 2–3 months.

FAMILY PARAGONIMIDAE

Trematodes in this family mainly have a flattened fleshy body and a tegument covered with spines. The oral sucker is subterminal and the ventral sucker is located around the middle of the body. The genital pore is situated just below the ventral sucker. Several genera are of local veterinary interest. *Paragonimus*, commonly referred to as the 'Lung fluke', is found in cats, dogs and other carnivores and in humans in North America and Asia. Pulmonary signs are comparatively rare in cats or dogs and the veterinary interest is in the potential reservoir of infection for humans.

Life cycle: The life cycle involves an amphibious or water snail, and a crayfish or freshwater crab. Snails of the genera *Melania*, *Ampullaria* or *Pomatiopsis* are infected by miracidia in which further development through sporocyst, redia and cerceria takes place. After escaping the snail, the cercariae swim about and, on contact with a freshwater crab or crayfish, penetrate it and encyst. Crabs and crayfish can also eat cercaria-infected snails. Infection of the final host occurs by ingestion of the metacercariae in the liver or muscles of the crustacean. Infection can also be acquired through consumption of paratenic hosts which have eaten infected crabs or crayfish. The young flukes migrate to the lungs where they are encapsulated by fibrous cysts connected by fistulae to the bronchioles to facilitate egg excretion. Eggs pass up from the lung in the

sputum, which the animal usually swallows such that eggs are passed in the faeces. The prepatent period is 5–6 weeks.

Paragonimus

Parasites of this genus are localised in the lungs of several vertebrate hosts (Table 1.53).

Paragonimus westermani

Description: The parasite is rounded (lemon-shaped) and thick (7.5–16 mm by 4–8 mm), reddish-brown in colour and covered in very small scale-like spines. The oral and ventral suckers are similar in size, with the ventral sucker situated slightly anterior to the middle of the fluke (Fig. 1.101). The testes are located in the posterior half of the body. Species differentiation is based on the shape of the spines. Those in *P. westermani* are large and have bifid points. Eggs are yellowish-brown in colour, operculate, 75–118 by 42–67 µm, and the shell is thickened at the opposite end to the operculum (Fig. 1.102).

Table 1.53 *Paragonimus* species.

Species	Hosts	Site	Intermediate hosts
Paragonimus westermani	Dogs, cats, pigs, goats, cattle, foxes, other carnivores, humans and primates	Lung	Snails of the genera *Melania*, *Ampullaria*, *Pomatiopsis* Crabs and crayfish
Paragonimus kellicotti	Cats, pigs, dogs	Lung	Snails of the genera *Melania*, *Ampullaria*, *Pomatiopsis* Crabs and crayfish

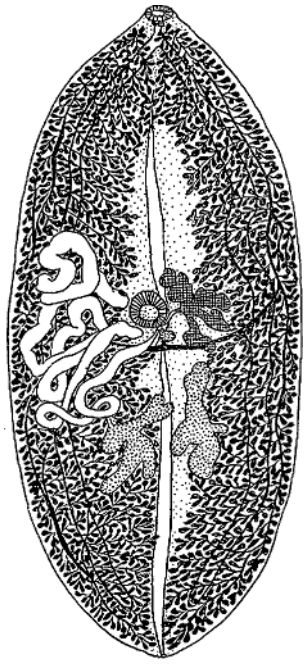


Fig. 1.101 *Paragonimus westermani*. (Adapted from Mönnig, 1934.)

Paragonimus kellicotti

Description: Adult flukes are usually located in pairs in cysts in the lungs of the final host. The parasite is rounded, reddish-brown in colour, 7.5–16 by 4–8 mm and covered in scale-like spines. The ventral sucker is situated slightly anterior to the middle of the fluke. Species differentiation is based on the shape of the spines. Those in *P. kellicotti* are very large and have a number of points. Eggs are golden-brown in colour, 80–118 by 48–60 µm, and have a partly flattened operculum.

FAMILY NANOPHYETIDAE

The genus *Nanophyetus* is a fluke found mainly in the small intestine of dogs, mink and other fish-eating mammals. It occurs in the north-west USA and parts of Siberia and is of importance because the flukes are vectors of the rickettsial organism *Neorickettsia helminthoeca*, which causes severe haemorrhagic enteritis of dogs, so-called 'salmon poisoning'. This name is derived from the cycle of the fluke, which involves a water snail and a fish that is often one of the salmonid type.

Life cycle: Undeveloped eggs are passed in the faeces of the host and after hatching, which takes about three months, infect the snail first intermediate host where cercariae develop in rediae. The liberated cercariae swim for a while before penetrating a fish and encysting in the kidneys, muscles and other organs. Infection of the final host occurs when the fish is eaten. The prepatent period is as short as five days in the dog.

Nanophyetus

The main species is *Nanophyetus salmincola* (syn. *Troglotrema salmincola*) which infects the small intestine of dogs, foxes, cats, raccoons, mink, bears, lynxes, other fish-eating mammals and, rarely, humans. This parasite has snails (*Oxytrema*, *Goniobasis*, *Semisulcospira* spp.), salmonid fishes, other fish and salamanders as intermediate hosts.

Nanophyetus salmincola

Synonym: *Troglotrema salmincola*

Description: These trematodes are generally very small, oval or elongate, and white or cream in colour. Adult flukes measure about 1–2.5 mm long by 0.3 mm wide. The oral sucker is well developed and is located terminally and the ventral sucker is usually found in the mid-third of the body. The large testes are oval and situated side by side in the posterior third of the segment. The spherical ovary is situated behind the ventral sucker and to its right. The genital pore is just to the posterior of the ventral sucker and the cirrus sac is large. The vitellaria consist of large follicles. Eggs are yellowish-brown in colour, unembryonated and measure about 64–80 by 34–50 µm. They have an indistinct operculum and a small rounded abopercular knob at the opposite pole.

FAMILY COLLYRICLIDAE

Parasites of the genus *Collyriclum* occur within subcutaneous cysts in chickens, turkeys and wild birds. Intermediate hosts are snails and dragonflies.

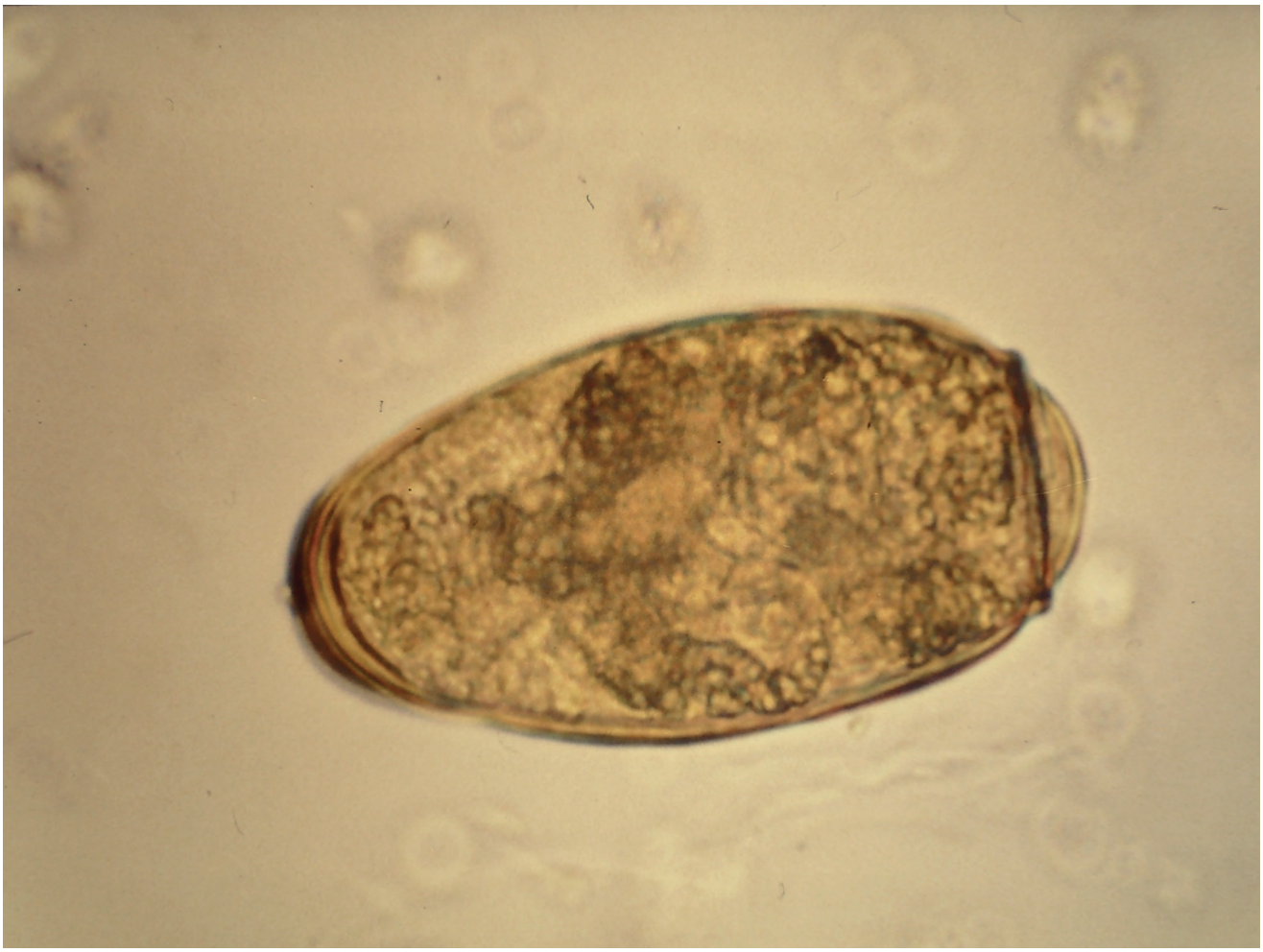


Fig. 1.102 *Paragonimus westermani* egg.

Life cycle: Cysts in the subcutaneous tissues usually contain a pair of flukes. Eggs are passed through an opening in the wall of the cyst and hatch in the environment to produce a miracidium, which penetrates a snail. These directly produce cercariae, there being no redial development, and the cercariae are shed from the snail and will enter dragonfly larvae, where they encyst to the metacercaria stage. Infection of the final host occurs through ingestion of the infected dragonfly. The immature trematodes then migrate to the subcutaneous tissues.

Collyriclum

The main species is *Collyriclum faba* (syn. *Monostoma faba*) which infects the skin and subcutaneous tissues of chickens, turkeys and wild birds. This parasite has snails and dragonfly nymphs as intermediate hosts.

Collyriclum faba

Synonym: *Monostoma faba*

Description: The flukes occur in pairs in a tissue cyst. The fluke has a spiny tegument, is dorsally convex and venterally flattened, and measures about 4 by 5 mm. There is no ventral sucker and the oral sucker is small. The ovary is multilobular and the vitellaria are located in the anterior half of the body. Eggs are very small, measuring about 19–21 by 9–11 µm.

FAMILY PROSTHOGONIMIDAE

Prosthogonimus are parasites found in the cloaca and reproductive tract of birds.

Life cycle: Eggs passed in faeces hatch to produce a miracidium, which penetrates a snail to form a mother sporocyst, which produces daughter sporocysts. These directly produce cercariae, there being no redial development, and the cercariae are shed from the snail and will enter dragonfly larvae via the rectal respiratory chamber where they eventually encyst as the metacercaria stage in the haemocoel. Infection of the final host occurs through ingestion of the infected nymphal stage or the adult dragonfly. The immature trematodes then migrate to the cloaca and bursa of Fabricius or enter the oviduct. The fluke is mature after about a week.

Prosthogonimus

Parasites of this genus infect several bird species (Table 1.54)

Table 1.54 *Prosthogonimus* species.

Species	Hosts	Site	Intermediate hosts
Prosthogonimus pellucidus (syn. *Prosthogonimus intercalandus*, *Prosthogonimus cuneatus*)	Chickens, turkeys, other fowl, geese, ducks	Cloaca, oviduct, bursa of Fabricius	Water snails (*Bithynia*) Dragonfly nymphs
Prosthogonimus macrorchis	Chickens, turkeys, other fowl, ducks	Lower gut, cloaca, oviduct, bursa of Fabricius	Water snails (*Bithynia*) Dragonfly nymphs
Prosthogonimus ovatus	Chickens, turkeys, other fowl, geese	Cloaca, oviduct, bursa of Fabricius	Water snails (*Bithynia*) Dragonfly nymphs

Prosthogonimus pellucidus

Synonyms: *Prosthogonimus intercalandus*, *Prosthogonimus cuneatus*

Description: Adult flukes are pear-shaped, semi-transparent, pale orange when fresh and measure around 9–12 mm in length, being broader towards the posterior. The fluke has a spiny cuticle and two suckers are present. The posterior width of the fluke increases from the middle region. The ovoid eggs are around 26–32 by 10–15 µm in size, dark brown and have a small spine at the opposite pole to the operculum.

Prosthogonimus macrorchis

Description: These flukes are very similar to *P. pellucidus* but possess larger testes.

Prosthogonimus ovatus

Description: Adult flukes are smaller than the other two species, measuring 3–6 mm. The testes are slightly elongate and lie side by side in the midline.

FAMILY PLAGIORCHIIDAE

Plagiorchis are parasites of birds and are mainly located in the gut. One species, *P. arcuatus*, has a similar pathogenesis to *Prosthogonimus*, affecting the bursa of Fabricius in young birds and the oviduct in older birds.

Life cycle: The life cycle involves two intermediate hosts, namely freshwater snails and larvae of dragonflies. The definitive host is infected through eating the dragonflies or their nymphs containing encysted metacercariae.

Plagiorchis

The main species is *Plagiorchis arcuatus* which infects the oviduct and bursa of Fabricius of chickens and other poultry. This parasite has snails, crustacea and insects as intermediate hosts.

Plagiorchis arcuatus

Description: The fluke is oval, about 4–5 mm in length and 1.5 mm in breadth, and tapers to a point at both ends. The cuticle possesses small spines, which are more numerous in the anterior region. The testes are rounded or oval and lie obliquely behind each other. The ovary is rounded, situated near the end of the cirrus sac, and to the right of the ventral sucker.

FAMILY LECITHODENDRIIDAE

The Lecithodendriidae include the genera *Novetrema*, *Odeningotrema*, *Phaneropsolus* and *Primatotrema*, which are intestinal flukes of primates.

FAMILY OPISTHORCHIIDAE

The members of this family require two intermediate hosts, the first being water snails and the second a wide variety of fish, in which the metacercariae are encysted. The final hosts are fish-eating mammals in which they inhabit the bile ducts. These oval or fusiform flukes are of medium size and possess suckers which are small and weak and located fairly close together. The ovary and uterus are anterior to the testes. This feature avoids confusion with the similarly sized and shaped dicrocoeliid flukes where they are positioned posteriorly to the testis. *Clonorchis* is by far the most important genus, with *Apophallus*, *Cryptocotyle*, *Opisthorchis*, *Metorchis*, *Parametorchis* and *Pseudamphistomum* being of lesser importance.

Apophallus

Parasites of this genus are localised in the small intestine of gulls, cormorants, dogs, cats, foxes and seals. Fishes are the intermediate hosts.

Apophallus muhlingi

Synonym: *Cotylophallus muhlingi*

Description: Adult flukes are small and measure 1.2–1.6 mm by 0.2 mm. The cuticle is covered in fine spines. The suckers are small, equal in size and located in the midbody. The testes are rounded and lie diagonally one behind the other. The ovary is rounded and is opposite the anterior testis.

Apophallus donicum

Synonym: *Rossicotrema donicum*

Description: Flukes are small, measuring 0.5–1.15 mm by 0.2–0.4 mm. The cuticle is covered in spines and the testes are round and large and located in the posterior section of the body.

Cryptocotyle

The main species is *Cryptocotyle lingua* which infects the small intestine of gulls, terns, kittiwakes, seals, mink, dogs, cats and humans. This parasite has shellfish, snails and fish as intermediate hosts.

Cryptocotyle lingua

Description: Spatula-shaped body, 0.5–2 mm long by 0.2–0.9 mm wide. The cuticle is armed with spines and the suckers are small, with the anterior larger than the ventral sucker. The testes are slightly lobed and lie side by side or diagonally at the posterior end of the body. The ovary is trilobed and lies in front of the testes.

Clonorchis

The main species is *Clonorchis sinensis* (syn. *Opisthorchis sinensis*) which infects the bile ducts, pancreatic ducts and occasionally small intestine of humans, dogs, cats, pigs, mink, weasels and badgers. This parasite has operculated snails (*Parafossalurus*, *Bulimus* spp., *Bithynia*, *Melania* and *Vivipara*) and cyprinid fishes as intermediate hosts.

Clonorchis sinensis

Synonym: *Opisthorchis sinensis*

Description: The adult fluke is flat, transparent–pinkish, wide posteriorly and tapering anteriorly, and may reach a size of 25 mm long by 5 mm wide (Fig. 1.103). The cuticle is spiny in the young fluke but smooth in the adult. The testes are multibranched and posterior to the ovary and uterus. A cirrus sac is absent. Eggs have a thick, light yellowish-brown wall and measure 27–35 by 12–20 µm; they contain a miracidium when they are laid, the internal structure of which is asymmetrical. The convex operculum of the egg slots into a prominent rim of the shell (Fig. 1.104). A small hook-like structure is frequently present on the opposite pole.

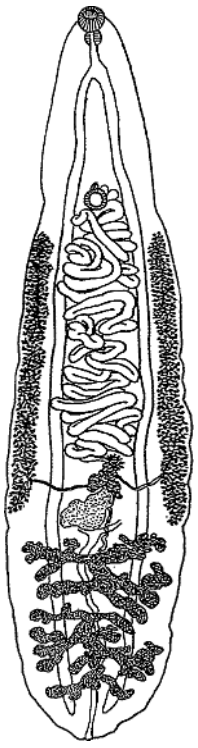


Fig. 1.103 *Clonorchis sinensis*. (Soulsby, 1971. Reproduced with permission from Lord Soulsby of Swaffham Prior.)

Fig. 1.104 *Clonorchis sinensis* egg.

Life cycle: The eggs normally hatch only after they have been swallowed by the snail first intermediate host. In the snails, the miracidium develops into a sporocyst, which produces rediae and these in turn produce cercariae, which have fairly long tails and elongate bodies with pigmented eye-spots. After breaking out of the snail, the cercaria swims about and on meeting a suitable fish, it penetrates partly or completely into the tissues of the fish and, losing its tail, becomes encysted in the fish. Infection of the final host occurs through eating raw infected fish. The metacercariae are liberated in the duodenum of the final host and reach the liver by way of the bile duct. The prepatent period is 16 days.

Opisthorchis

The main species is *Opisthorchis felineus* (syn. *Opisthorchis tenuicollis*, *Opisthorchis viverrini*) which infects the liver, bile ducts and occasionally pancreatic ducts of cats, dogs, foxes, pigs, humans and cetaceans. This parasite has freshwater snails (*Bithynia* spp.) and freshwater fish as intermediate hosts.

Opisthorchis felineus

Synonyms: *Opisthorchis tenuicollis*, *Opisthorchis viverrini*

Description: Adult flukes are reddish in colour, with a smooth cuticle and measure 7–12 by 1.5–2.5 mm (Fig. 1.105). The testes are lobed and not branched. Eggs are about 26–30 by 11–15 µm in size, and contain a miracidium when they are laid, the internal structure of which is asymmetrical. The operculum of the egg fits into a prominent rim of the shell and may have a tubercular appendage (Fig. 1.106).

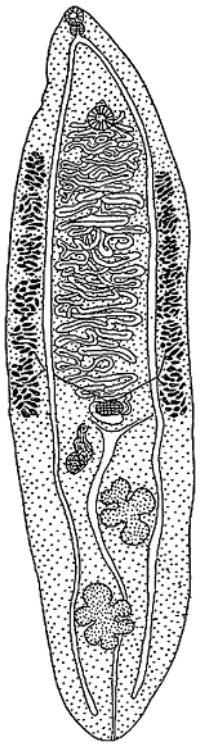


Fig. 1.105 *Opisthorchis felineus*. (Adapted from Mönnig, 1934.)

Fig. 1.106 *Opisthorchis felineus* egg.

Life cycle: The prepatent period is 2–3 weeks and deposited eggs are ingested by a snail in which cercariae develop in rediae. The cercariae encyst in fish as metacercariae and infect the definitive host when ingested. See **life cycle 20**.

Metorchis

Parasites of this genus are localised in the liver, bile ducts and gall-bladder of dogs, cats, foxes, seals, some poultry, mink, raccoons and occasionally humans (*Metorchis albidus*).

Metorchis albidus

Synonyms: *Distoma albicum*, *Opisthorchis albidus*

Description: The fluke is spatulate, pointed anteriorly, rounded and flat posteriorly, 2.5–6.5 mm long by 1–1.6 mm broad with a spinous cuticle in the young fluke. The genital pore is in front of the ventral sucker. The testes are located diagonally in the posterior region of the body and they are lobed. The ovary is fairly circular and lies just in front of the anterior testis. The operculate eggs are small, 24–30 by 13–16 µm.

Metorchis conjunctus

Description: Adults measure 1–6.5 mm long by 0.6–2.6 mm broad. The suckers are equal in diameter. The genital pore lies at the anterior margin of the acetabulum. The cuticle of the young fluke possesses spines.

Parametorchis

The main species is *Parametorchis complexus* which infects the liver and bile ducts of cats and dogs. The intermediate hosts of this parasite are not known, but probably are freshwater snails.

Parametorchis complexus

Description: The fluke is 5–10 mm long by 1.5–2 mm broad. The uterus forms a rosette around the ventral sucker. The testes are lobed and lie together in the posterior part of the body. The vitelline glands are restricted to the anterior third of the fluke.

Pseudamphistomum

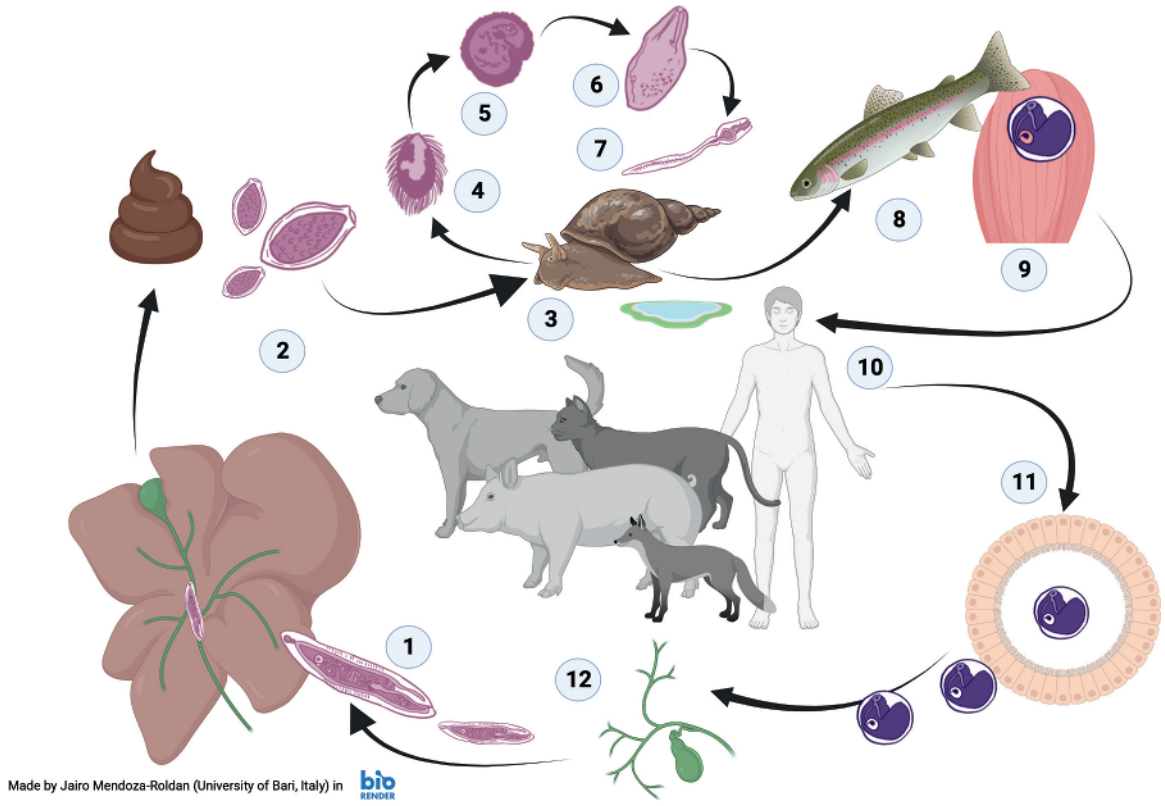
The main species is *Pseudamphistomum truncatum* which infects the liver and bile ducts of dogs, cats, foxes and rarely humans. This parasite has snails and fish as intermediate hosts.

Pseudamphistomum truncatum

Description: Adult flukes are small, measuring 2–2.5 mm, with a spiny body that is truncate posteriorly. The testes are spherical and lie horizontally at the posterior end of the body (Fig. 1.107).

LIFE CYCLE 20. LIFE CYCLE OF *OPISTHORCHIS FELINEUS*

The parasite lives in the biliary and pancreatic ducts (1) and occasionally in the small intestinal lumen of the definitive host, which includes fish-eating mammals such as dogs, cats, foxes, seals, lions, wolverines, martens, polecats and humans, but also pigs and rabbits. The eggs (2) are excreted with the faeces, and are ingested by aquatic snails (3) that act as first intermediate hosts. In the snail, the egg hatches to release a miracidium (4), that subsequently becomes a sporocyst (5), rediae (6) and then cercariae (7). The latter are highly motile and actively leave the first intermediate host to seek out a freshwater fish, the second intermediate host (8). On penetrating the fish skin, the cercariae lose their tails and become encysted in muscular tissues as metacercariae (9). When a susceptible definitive host ingests raw or undercooked fish containing the metacercariae (10), these hatch in the duodenum (11) and migrate to the liver via the biliary ducts (12), where the parasites mature to adult trematodes (1). The prepatent period is ~16 days.



ORDER STRIGEIDIDA

FAMILY BRACHYLAEMIDAE

Members of this family are parasites of birds (*Brachylaemus*), sheep (*Skrjabinotrema*) and pigs (*Postharmostomum*). The intermediate hosts are snails. They are of only minor veterinary importance.

Skrjabinotrema

The main species is *Skrjabinotrema ovis* which infects the small intestine of sheep. This parasite has snails as intermediate hosts.

Skrjabinotrema ovis

Description: Adult flukes are small with smooth bodies and measure about 1 mm long by 0.3–0.7 mm wide. Eggs measure 24–32 by 16–20 µm and are slightly flattened on one side with a large operculum at one end and a small appendage at the other.

Postharmostomum

The main species is *Postharmostomum suis* which infects the small intestine of pigs. This parasite has snails as intermediate hosts.

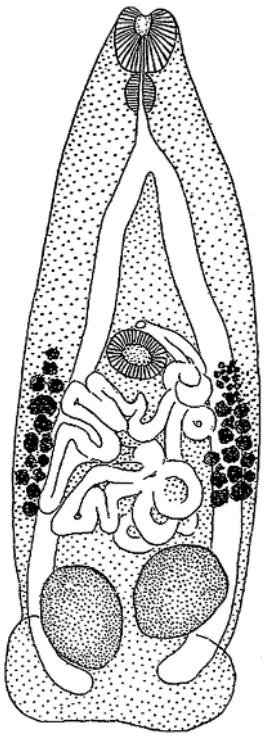


Fig. 1.107 *Pseumdamphistomum truncatum*. (Adapted from Mönnig, 1934.)

Postharmostomum suis

Description: The body is smooth, elongate and around 4–8 mm in length.

FAMILY HETEROPHYIDAE

These are small trematodes found in the intestines of mammals and birds. The genital pore and ventral sucker are located in a ventrogenital sac. More than 10 species of the family Heterophyidae have been reported in humans and fish-eating mammals. The life cycle generally involves two intermediate hosts, namely freshwater snails and fishes or frogs. Genera of veterinary interest are *Heterophyes* found in dogs, cats, foxes and humans; *Metagonimus* in the small intestines of dogs, cats, pigs and humans; *Cryptocotyle* of seabirds, reported in dogs and cats; and *Apophallus* (*Rossicotrema*) normally found in seabirds or seals but also reported in cats, dogs and foxes.

Heterophyes

Parasites of this genus are localised in the small intestine of dogs, cats, foxes and humans. Snails of the genus *Pirenella* and *Cerithida*, and fish are intermediate hosts.

Heterophyes heterophyes

Description: This is a small pear-shaped fluke that is wider posteriorly than anteriorly, measuring 1–1.7 mm by 0.3–0.7 mm. The ventral sucker is anterior to the middle of the body and the genital sucker lies immediately behind it and to one side and bears an incomplete circle of 70–80 small rods. The testes are located horizontally and are oval in shape (Fig. 1.108).

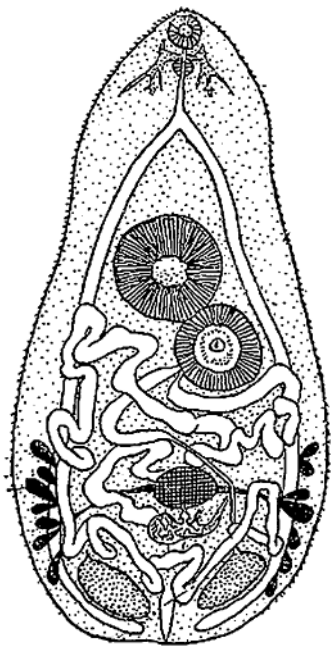


Fig. 1.108 *Heterophyes heterophyes*. (Neveu-Lemaire, 1936. Reproduced with permission from Editions Vigot.)

Heterophyes nocens

Description: Small ovoid fluke measuring 0.8–1 mm in length by 0.5–0.6 mm in width. The genital sucker is armed with 50–60 small rods and is located close to the ventral sucker.

Metagonimus

The main species is *Metagonimus yokagawai* which infects the small intestine of dogs, cats, pigs and humans. This parasite has snails (*Semisulcospira* spp.), cyprinid fish, mullet and trout as intermediate hosts.

Metagonimus yokagawai

Description: Small flukes that are wider posteriorly than anteriorly, measuring 1–2.5 mm by 0.4–0.7 mm. The cuticle bears spines over its whole surface. The ventral sucker is right of the median line and close to the genital pore, which opens anteriorly. The testes are slightly oblique and the ovary is median in position.

FAMILY SCHISTOSOMATIDAE

This family is primarily parasitic in the blood vessels of the alimentary tract and bladder. In humans, schistosomes are often responsible for severe and debilitating disease and veterinary interest lies in the fact that they can cause a similar disease in animals, some of which may act as reservoirs of infection for humans. The schistosomes differ from other flukes in that the sexes are separate, the small adult female lying permanently in a longitudinal groove, the gynaecophoric canal, in the body of the male (Fig. 1.109). The most important genus is *Schistosoma*, with *Bilharziella*, *Trichobilharzia*, *Orientobilharzia*, *Ornithobilharzia*, *Heterobilharzia* and *Austrobilharzia* other genera of lesser importance.

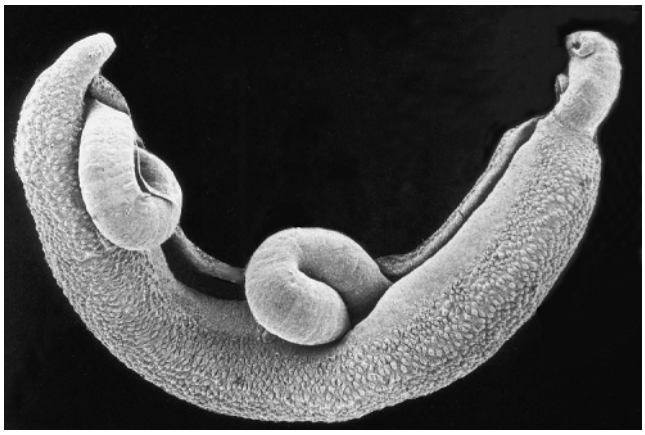


Fig. 1.109 Male and female *Schistosoma* in copula.

Schistosoma

The sexes are separate, with the male, which is broad and flat and about 2 cm long, carrying the slender female in the hollow of its inwardly curved body. This characteristic and the vascular predilection site are sufficient for generic identification. Suckers are either absent or weak and there is no pharynx. The genus, as currently defined, is paraphyletic so revisions are likely. The genus has been divided into four groups: *haematobium*, *indicum*, *mansoni* and *japonicum*. Species found in Africa are divided into two groups: those with a lateral spine on the egg (*mansoni* group) and those with a terminal spine (*haematobium* group) (Fig. 1.110; Table 1.55).

Schistosoma bovis

Description: The male is 9–22 mm long and 1–2 mm wide, and the female 12–28 mm long. In the male, the suckers and the tegument behind the suckers are armed with minute spines, while the dorsal surface of the tegument bears small cuticular tubercles. The slender female worm lies permanently in a ventral groove in the broad flat body of the male. The eggs are usually spindle-shaped, but smaller eggs may be oval and have a mean measurement of 187 by 65 µm when passed in the faeces. There is no operculum.

Life cycle: The ovigerous female penetrates deeply into the small vessels of the mucosa or submucosa of the intestine and inserts her tail into a small venule. Since the genital pore is terminal, the eggs are deposited, or even pushed, into the venule. There, aided by their spines and by proteolytic enzymes secreted by the unhatched miracidia, they penetrate the endothelium to enter the intestinal submucosa and ultimately the gut lumen; they are then passed out in the faeces. Worms present in the vesical veins penetrate the endothelial lining of the bladder where eggs may be passed in the urine. Some eggs are carried away in the bloodstream and locate in other organs such as the liver. The eggs hatch in water and the miracidia penetrate appropriate snails. Cercariae develop from daughter sporocysts, which replace the redia stage, and there is no metacercarial phase; penetration of the final host by the motile cercariae occurs via the skin or by ingestion in drinking water. After penetration or ingestion, the cercariae lose their forked tails, transform to schistosomula or young flukes, and travel via the bloodstream through the heart and lungs to the systemic circulation. In the liver, they locate in the portal veins and become sexually mature before migrating to their final site, the mesenteric veins. The prepatent period is 6–7 weeks.

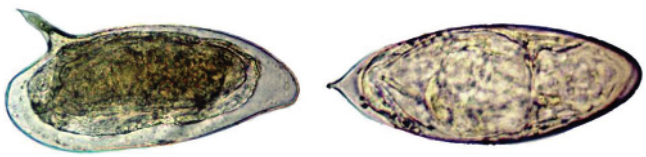


Fig. 1.110 *Schistosoma* egg morphology: (a) *mansoni* group; (b) *haematobium* group.

Table 1.55 *Schistosoma* species.

Species	Hosts	Site	Intermediate hosts
Haematobium *group*			
Schistosoma bovis	Cattle, sheep, goats, camels	Portal, mesenteric and urogenital veins	Snails (*Bulinus* spp., *Physopsis* spp.)
Schistosoma haematobium	Humans, primates	Bladder veins and urethra	Snails (*Bulinus* spp.)
Schistosoma mattheei	Cattle, sheep, goats, camels, humans, primates	Portal, mesenteric and bladder veins	Snails (*Physopsis* spp.)
Schistosoma leiperi	Cattle, antelopes	Mesenteric veins	Snails (*Bulinus* spp.)
Indicum *group*			
Schistosoma indicum	Cattle, buffalo, sheep, goats, horses, donkeys, camels	Portal, pancreatic, hepatic and mesenteric veins	Snails (*Indoplanorbis*)
Schistosoma nasale (syn. *Schistosoma nasalis*)	Cattle, goats, sheep, buffalo, horses	Nasal mucosa veins	Snails (*Lymnaea* spp., *Indoplanorbis* spp.)
Schistosoma spindale	Cattle, buffalo, horses, pigs and rarely dogs	Mesenteric veins	Snails (*Planorbis* spp., *Indoplanorbis* spp., *Lymnaea* spp.)
Mansoni *group*			
Schistosoma mansoni	Humans, primates, wild animals	Mesenteric veins	Snails (*Biomphalaria* spp.)
Japonicum *group*			
Schistosoma japonicum	Cattle, horses, sheep, goats, dogs, cats, rabbits, rodents, pigs, humans	Portal and mesenteric veins	Snails (*Oncomelania* spp.)
Others			
Schistosoma incognitum (syn. *Schistosoma suis*)	Pigs, dogs	Mesenteric veins	Snails (*Radix* spp.)
Schistosoma turkestanica (syn. *Orientobilharzia turkestanicum*)	Cattle, buffalo, sheep, goats, camels, horses, donkeys, cats	Mesenteric veins and small veins of the pancreas and liver	Snails (*Lymnaea* spp.)

Schistosoma mattheei

Description: The male flukes measure around 9–22 mm in length and about 1–2 mm wide. Females range from 12 to 28 mm in length. The body of the male behind the suckers is armed with very long spines, as are the suckers. The dorsal surface possesses small

cuticular tubercles. The eggs passed in faeces are usually spindle-shaped, but smaller ones may be oval. They measure 170–280 by 72–84 µm. There is no operculum.

Schistosoma indicum

Description: The sexes are separate; the males are 5–19 mm and the females 6–22 mm in length. The eggs are oval with a terminal spine and measure 57–140 by 18–72 µm.

Schistosoma spindale

Description: The male measures 5–16 mm and the female 7.2–16.2 mm long. The sexes are separate, with the male, which is broad and flat and up to about 1.5 cm in length, carrying the female in the hollow of its inwardly curved body. The eggs are spindle-shaped, measure 200–300 by 70–90 µm and have a lateral or terminal spine. There is no operculum.

Schistosoma nasale

Synonym: *Schistosoma nasalis*

Description: The sexes are separate. The male, which is broad and flat and about 0.6–1 cm long, carries the female in the hollow of its inwardly curved body. The flukes closely resemble those of *S. spindale*. The eggs measure 350–380 by 50–80 µm and are boomerang-shaped, with a terminal spine.

Life cycle: Details of the life cycle are not completely known. The female in the veins of the nasal mucosa lays her eggs, which presumably enter the nasal sinuses and are sneezed out. The eggs hatch in minutes in water and the miracidia penetrate appropriate snails. Development to the cercarial stage occurs without a redial form and there is no metacercarial phase. After penetration or ingestion, the cercariae transform to schistosomula, or young flukes, and travel to their final site, the nasal veins.

Schistosoma mansoni

Description: The adult male is up to 10 mm in length and possesses a longitudinal groove, the gynaecophoric canal, that enfolds the female, which is longer (12–16 mm) and thinner. The tegument of the male has tubercles on the dorsal surface, whereas the tegument of the female is smooth. The male has 6–9 testes, and the male genital pore opens ventrally, immediately posterior to the ventral sucker. The female possesses a single ovary located in the anterior portion of the body.

Schistosoma japonicum

Description: The male is broad and flat and 9.5–20 mm long, carrying the female (12–26 mm long) in the hollow of the inwardly curved body. The suckers lie close together near the anterior end. The cuticle is spiny on the suckers and in the gynaecophoric canal. This characteristic and the vascular predilection site are sufficient for generic identification. The eggs are short, oval, measuring 70–100 by 50–80 µm, and may have a small lateral subterminal spine. There is no operculum.

Life cycle: This is similar to that of *S. bovis*. Development to the cercarial stage occurs through two generations of sporocyst without a redial form and there is no metacercarial phase, penetration of the final host by the motile cercariae occurring via the skin. The developmental period in the snail can be as short as five weeks. Schistosomula, or young flukes, that reach the abdominal vessels and pass to the portal veins become sexually mature in about four weeks.

Schistosoma turkestanica

Synonym: *Orientobilharzia turkstanicum*

Description: This is a small species; the male is 4.2–8 mm and the female 3.4–8 mm in length. The spirally coiled ovary is positioned in the anterior part of the body. In the male there are around 70–80 testes. The female uterus is short and contains only one egg at a time, which measures 72–77 by 16–26 µm with a terminal spine and a short appendage at the opposite end.

OTHER SCHISTOSOMES

The main species is *Bilharziella polonica* which infects the mesenteric and pelvic veins of ducks. This parasite has snails of the genus *Planorbis* as intermediate hosts.

Bilharziella polonica

Description: The body is lancet-shaped posteriorly and the sexes are separate. Males are about 4 mm and females 2 mm in size. The female genital pore is just behind the ventral sucker and the short uterus contains one egg at a time. The eggs have a long, narrow and elongate anterior end and a swollen posterior end with a terminal spine, and measure 400 by 100 µm.

Life cycle: Eggs are laid in the small vessels of the intestinal wall through which they penetrate and are passed out in the faeces. Development takes place in the snail intermediate host and leads to the release of cercariae, which infect the intermediate host either percutaneously or following ingestion.

FAMILY DIPLOSTOMATIDAE

The family Diplostomatidae includes the genera *Alaria* and *Diplostomum*, which are flukes of mammals and birds. Only the former genus is of veterinary significance. The life cycle involves two intermediate hosts, namely freshwater snails and frogs. The definitive host is infected through eating frogs containing encysted metacercariae (mesocercariae).

Alaria

Alaria are found in the small intestine of dogs, cats, foxes and mink (Table 1.56). The anterior forebody of the fluke is flattened or spoon-shaped, and the posterior hindbody is conical and contains

Table 1.56 *Alaria* species.

Species	Hosts	Site	Intermediate hosts
Alaria alata	Dogs, cats, foxes, mink, wild carnivores and rarely humans	Small intestine	Snails (*Planorbis* spp.), frogs, toads Paratenic: snakes, rodents
Alaria americana	Dogs, foxes and other canids	Small intestine	Snails (*Planorbis* spp.), frogs, toads
Alaria canis	Dogs, foxes	Small intestine	Snails (*Heliosoma* spp.), frogs, toads
Alaria marcianae	Cats, raccoons	Small intestine	Snails (*Heliosoma* spp.), frogs, toads Paratenic: snakes, rodents
Alaria michiganensis	Dogs, foxes, coyotes	Small intestine	Snails (*Planorbis* spp.), frogs, toads

the reproductive organs. The oral and ventral suckers are located in the forebody. The life cycle involves freshwater snails as first intermediate hosts, and amphibians or reptiles as second intermediate hosts.

Life cycle: Unembryonated eggs are passed in the faeces from which miracidia eventually hatch and enter freshwater snails (*Planorbis*). Sporocysts produce cercariae with bifurcated tails. These leave the snail and infect tadpoles or frogs where the cercariae encyst in the muscles, forming mesocercariae. If a frog, snake or mouse eats the tadpole, the mesocercariae become encysted, these animals acting as paratenic hosts. Dogs and foxes may be infected by eating rodents infected with mesocercariae. Once infected, the mesocercariae migrate extensively, including passage through the lungs and diaphragm, becoming metacercariae before returning to the small intestine and maturing into flukes. The prepatent period is 2–4 weeks.

Alaria alata

Description: Adult flukes are 2–6 mm in length and the flat, spoon-shaped, expanded anterior part is much longer than the posterior cylindrical hindbody which contains the reproductive organs. At the anterior lateral corners of the anterior part, there are two tentacle-like processes (Fig. 1.111). The suckers are very small and the adhesive organ consists of two long folds with distinct lateral margins. The yellowish-brown eggs are large, 98–134 by 62–68 µm, operculate and unembryonated (Fig. 1.112).

Alaria americana

Description: Adult flukes range from 2.5 to 4 mm in length. The genital pore is located posteriorly on the mid-hindbody. This species is additionally characterised by the presence of pointed processes flanking the oral sucker.

Alaria canis

Description: Adult flukes are 2.5–4.2 mm long. There is a conical tentacle-like appendage on each side of the oral sucker. There is an oval holdfast organ with a longitudinal median depression

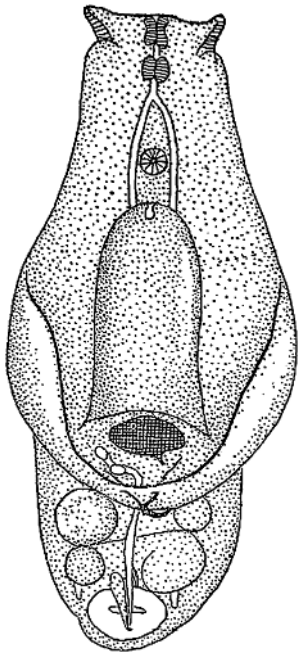


Fig. 1.111 *Alaria alata*. (Adapted from Baylis, 1929.)

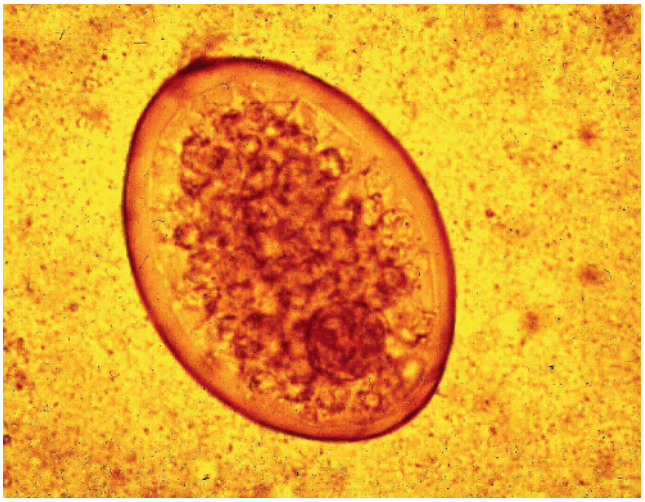


Fig. 1.112 *Alaria* egg.

extending from the ventral sucker to the constriction between the anterior and posterior parts of the body. Testes are lobed, with the posterior one much larger.

FAMILY STRIGEIDAE

These flukes are characterised by a constriction dividing the body into an anterior flattened adhesive organ and a posterior cylindrical or oval part, which contains the reproductive system. A cup-shaped adhesive organ is present in the anterior region. They are parasites of the alimentary tract of birds. The life cycle involves two intermediate hosts: freshwater snails of many genera and a second host that may be a fish or leech. Genera include *Apatemon* and *Cotylurus* in the intestine of pigeons and ducks, and *Parastrigea* in ducks.

Apatemon

The main species is *Apatemon gracilis* which infects the intestine of ducks, pigeons and wild birds. This parasite has snails and leeches as intermediate hosts.

Apatemon gracilis

Description: Adult flukes have a cup-like anterior region, containing an adhesive organ, and a posterior cylindrical region and measure 1.5–2.5 mm by 0.4 mm. The suckers are fairly well developed and the testes and ovary are arranged one behind the other with the ovary foremost. Vitellaria are limited to the posterior region of the body.

Parastrigea

The main species is *Parastrigea robusta* which infects the intestine of ducks. The intermediate host of this parasite is unknown.

Parastrigea robusta

Description: The flukes are 2–2.5 mm long and broader in the anterior region (1.5 mm) than the posterior region (1 mm). The genital papilla is large and oviform and the testes are compact and only slightly lobed. The vitellaria are mainly located in the adhesive organ and the lateral expansions, although some extend into the posterior part of the body.

Cotylurus

The main species is *Cotylurus cornutus* which infects the intestine of ducks, pigeons and wild birds. This parasite has snails as intermediate hosts.

Cotylurus cornutus

Description: The adult flukes are around 1.2–1.5 mm long and 0.5 mm wide with a rounded anterior region and an ovoid posterior region. The oral sucker is smaller than the ventral sucker and the testes and ovary are arranged one behind the other. They are similar to *Apatemon* species but a strong copulatory organ is located in the bursa.

CLASS CESTODA

This class differs from the Trematoda in having a tape-like body with no body cavity or alimentary canal. There is a wide variation in length, ranging from a few millimetres to several metres. The body is segmented, each segment containing one and sometimes two sets of male and female reproductive organs. Almost all the tapeworms of veterinary importance are in the order Cyclophyllidea, the two exceptions being in the order Pseudophyllidea.

ORDER CYCLOPHYLLIDEA

STRUCTURE AND FUNCTION

The adult cestode (Fig. 1.113) consists of a globular head or **scolex** bearing attachment organs, a short unsegmented neck and a chain of segments. The chain is known as a **strobila** and each segment as a **proglottid**. The organs of attachment are four suckers on the sides of the scolex and these may bear hooks. The scolex usually bears anteriorly a mobile protrusible cone or rostellum and in some species this may be armed with one or more concentric rows of hooks, which aid in attachment.

The proglottids are continuously budded from the neck region and become sexually mature as they pass down the strobila to the distal end of the tapeworm. Each proglottid is hermaphrodite with one or two sets of reproductive organs, the genital pores usually opening on the lateral margin or margins of the segment (Fig. 1.114); both self-fertilisation and cross-fertilisation between proglottids may occur. The structure of the genital system is generally similar to that of the trematodes. As the segment matures, its internal structure largely disappears and the fully ripe or gravid proglottid eventually contains only remnants of the branched uterus packed with eggs. The gravid segments are usually shed intact from the strobila and pass out with the faeces, either singly or occasionally in chains. Outside the body, the eggs are liberated by disintegration of the segment or are shed through the genital pore.

The fully embryonated egg consists of:

1. the hexacanth (six-hooked) embryo or **oncosphere**
2. a thick, dark, radially striated 'shell' called the **embryophore** (in the Mesocestoididae it is apparent as a thin cellular membrane)
3. a true shell, which is a delicate membrane and is often lost while still in the uterus.

The tegument of the adult tapeworm is highly absorptive, the worm deriving all its nourishment through this structure. Below the tegument are muscle cells and the parenchyma, the latter a syncytium of cells, which fills the space between the organs. The nervous system consists of ganglia in the scolex from which nerves run posteriorly

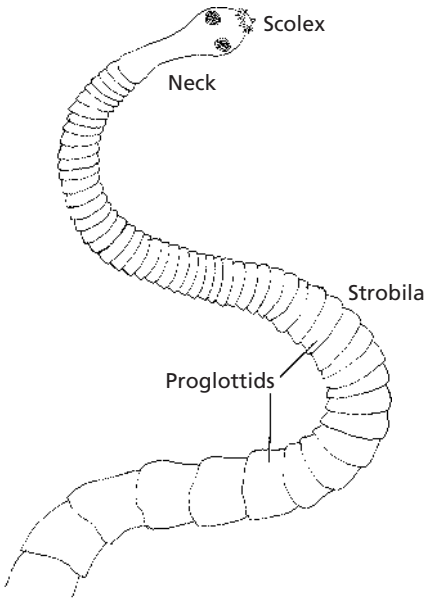


Fig. 1.113 Structure of a typical cyclophyllidean cestode.

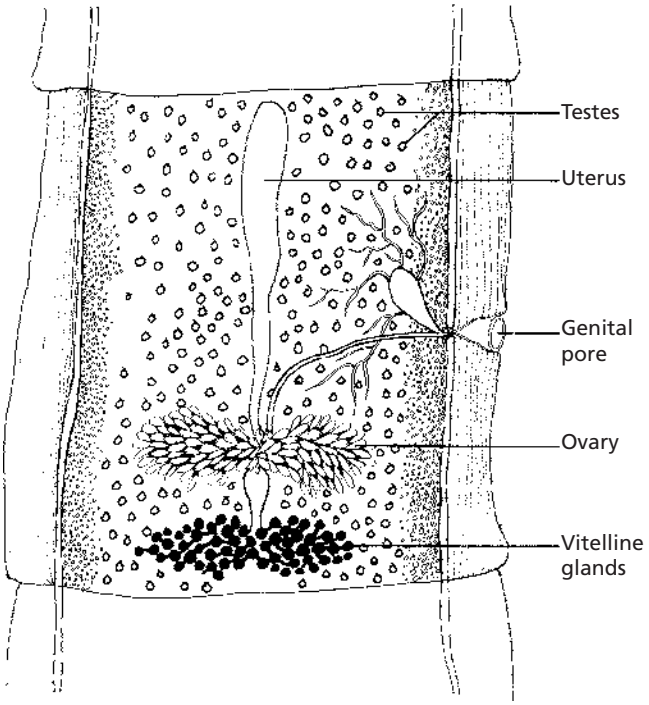


Fig. 1.114 Mature segment illustrating the reproductive organs.

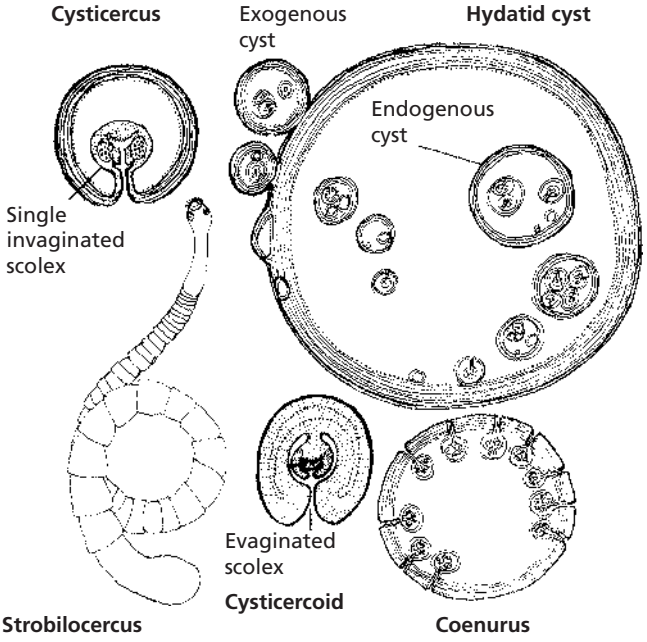


Fig. 1.115 Larval stages of cyclophyllidean cestodes.

and enter the strobila. The excretory system, as in the Trematoda, is composed of flame cells leading to efferent canals that run through the strobila to discharge at the terminal segment.

LIFE CYCLE

The typical life cycle of these cestodes is indirect with one or more intermediate hosts. With few exceptions, the adult tapeworm is found in the small intestine of the final host, the segments and eggs reaching the exterior in the faeces. When the egg is ingested by the intermediate host, the gastric and intestinal secretions digest the embryophore and activate the oncosphere. Using its hooks, it tears through the mucosa to reach the blood or lymph stream or, in the case of invertebrates, the body cavity. Once in its predilection site, the oncosphere loses its hooks and develops, depending on the species, into one of the following larval stages, often known as **metacestodes** (Fig. 1.115).

- **Cysticercus**: Single fluid-filled cyst or bladder containing an attached single invaginated scolex, sometimes called a protoscolex.
- **Coenurus**: This large cyst is similar to a cysticercus, but with numerous invaginated scolices attatched to the cyst wall.
- **Strobilocercus**: The scolex is evaginated and is connected to the cyst by a chain of segmented asexual proglottids. The latter are digested away after ingestion by the final host, leaving only the scolex.
- **Hydatid**: This is a large, fluid-filled, complex cyst lined with germinal epithelium from which are produced invaginated scolices which lie free or in bunches, surrounded by germinal epithelium (brood capsules). The contents of the cysts other than the fluid (i.e. scolices and brood capsules) are frequently described as 'hydatid sand'. Occasionally also, daughter cysts complete with cuticle and germinal layer are formed endogenously or, if the cyst wall ruptures, exogenously.
- **Cysticercoid**: A single evaginated scolex embedded in a small solid cyst. Typically found in very small intermediate hosts such as arthropods.
- **Tetrathyridium**: Worm-like, flattened and elongate larva with an invaginated acetabular scolex; found only in Mesocestoididae.

When the metacestode is ingested by the final host, the scolex attaches to the mucosa, the remainder of the structure is digested off and a chain of proglottids begins to grow from the base of the scolex.

The seven main families of veterinary interest in the order Cyclophyllidea are the Taeniidae, Anoplocephalidae, Dilepididae, Davaineidae, Hymenolepididae, Mesocestoididae and Paruterinidae.

FAMILY TAENIIDAE

The adults are, in most cases, large tapeworms and are found in domestic carnivores and humans in the small intestine. Genera of importance are *Taenia* (syn. *Multiceps*) and *Echinococcus*. The scolex has an armed rostellum with a concentric double row of hooks (the important exception is *Taenia saginata* whose scolex is unarmed). The gravid segments are longer than they are wide. The intermediate stage is a cysticercus, strobilocercus, coenurus or hydatid cyst and these occur only in mammals. Historically, the intermediate stage has been named according to the type of metacestode stage present in the intermediate host. Thus, *Cysticercus tenuicollis* found in the ruminant host is the metacestode stage of *Taenia hydatigena* in the dog. The correct nomenclature now is for the intermediate host stage to be referred to as the 'metacestode stage' of the adult *Taenia* species.

Taenia

Members of the genus *Taenia* are large tapeworms comprising a number of species (Table 1.57). Differentiation is usually based on the size of the scolex, the size of the rostellum and number of hooks, and on the morphology of the genital system within the mature proglottids.

Table 1.57 *Taenia* species.

Species	Final hosts	Intermediate hosts (larval stage)	Site
Taenia asiatica (syn. *Taenia saginata asiatica*)	Humans	Cattle	Muscle
Taenia crassiceps	Foxes, coyotes	Rodents	Abdominal cavity, various tissues
Taenia hydatigena (syn. *Taenia marginata*)	Dogs, foxes, wild canids, mustelids	Cattle, sheep, goats, pigs (*Cysticercus tenuicollis*)	Abdominal cavity, liver
Taenia multiceps (syn. *Multiceps multiceps*)	Dogs, foxes, wild canids	Sheep, cattle, goats, pigs, horses, deer, camels, humans (*Coenurus cerebralis*)	Brain, spinal cord
Taenia skrjabini		Sheep (*Coenurus skrjabini*)	Muscle, subcutaneous tissue
Taenia (*Multiceps*) *gaigeri*		Goat (*Coenurus gaigeri*)	
Taenia ovis (syn. *Taenia cervi*, *Taenia krabbei*, *Taenia hyaenae*)	Dogs, foxes, wild canids	Sheep, goats (*Cysticercus ovis*) Deer (*Cysticercus cervi*) Reindeer (*Cysticercus tarandi*) Camels (*Cysticercus dromedarii*, *Cysticercus cameli*)	Muscle
Taenia pisiformis	Dogs, foxes, wild canids	Rabbits, hares (*Cysticercus pisiformis*)	Peritoneum, liver
Taenia saginata (syn. *Taeniarhynchus saginata*)	Humans	Cattle, occasionally other ruminants (*Cysticercus bovis*)	Muscle
Taenia serialis (syn. *Multiceps serialis*)	Dogs	Rabbits, hares (*Coenurus serialis*)	Connective tissue
Taenia solium	Humans	Pigs, wild boar (*Cysticercus cellulosae*)	Muscle
Taenia taeniaeformis (syn. *Hydatigera taeniaeformis*, *Taenia crassicollis*)	Cats, wild felids	Small rodents (*Strobilocercus fasciolaris*; syn. *Strobilocercus crassicollis*)	Liver

The adults of *Taenia* are usually of minor importance in domesticated animals, and it is the larval stages which are of veterinary interest.

Taenia asiatica

Synonym: *Taenia saginata asiatica*

Description: Similar to *T. saginata*. The adult tapeworm is about 3.5 m long with a scolex bearing four simple suckers and the rostellum is usually surrounded by two rows of rudimentary hooklets. It is unique in having posterior protuberances in the gravid proglottid (which are absent in other taeniids, including *T. saginata*) and it presents 11–32 uterine buds. The metacestode differs morphologically from that of *T. saginata* in having wart-like formations on the external surface of the bladder wall.

Taenia hydatigena

Synonyms: *Taenia marginata*

Description: *Taenia hydatigena* is a large tapeworm measuring up to 5 m in length. The scolex is large and has two rows of 26 and 46 rostellar hooks. Four suckers are present. Gravid proglottids measure 12 by 6 mm and the uterus has 5–10 lateral branches. The mature metacestode (*Cysticercus tenuicollis*) is about 5–7 cm in diameter (see Fig. 9.26) and contains a watery fluid and invaginated scolex with a long neck. Eggs are subspherical or slightly elliptical and measure 36–39 by 31–35 µm. They have a smooth thick shell with a radially striated embryophore and contain a hexacanth embryo.

Life cycle: Dogs and wild canids are infested by consuming the cysticercus in the intermediate host. The intermediate host is infected through the ingestion of tapeworm eggs that hatch in the intestine. The oncospheres, infective to sheep, goats, cattle and pigs, are carried in the blood to the liver in which they migrate for about four weeks before they emerge on the surface of this organ and attach to the peritoneum. Within a further four weeks, each develops into the characteristically large metacestode, *Cysticercus tenuicollis*. The complete life cycle of this tapeworm is around 7–8 months. See **life cycle 21**.

Taenia multiceps

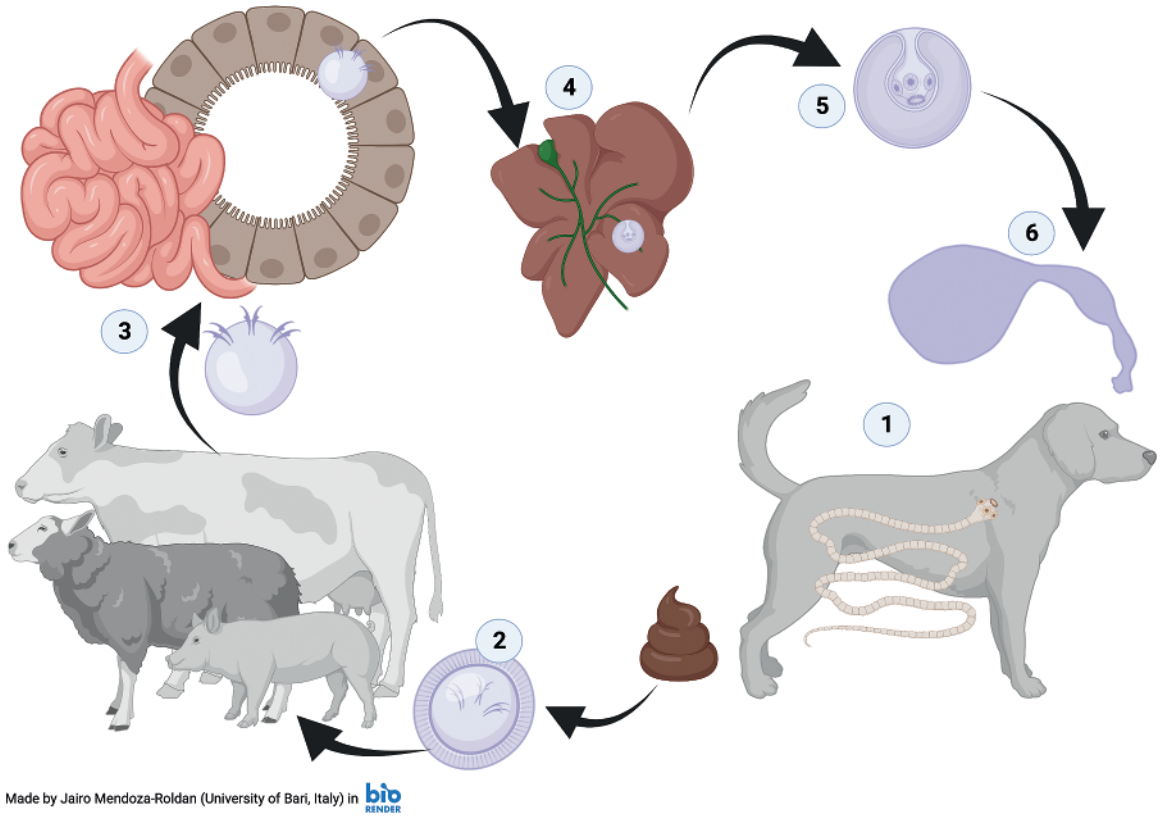
Synonyms: *Multiceps multiceps*, *Coenurus cerebralis*, *Taenia skrjabini*, *Coenurus skrjabini*, *Taenia* (*Multiceps*) *gaigeri*, *Coenurus gaigeri*

Description: Adult tapeworms are 40–100 cm in length and have a small head about 0.8 mm in diameter with four suckers (Fig. 1.116). There is a double ring of 22–32 rostellar hooks (Fig. 1.117). The gravid segments measure 8–12 mm by 3–4 mm and the uterus has 18–26 lateral branches which contain taeniid eggs. Eggs are approximately 29–37 µm in diameter and have thick smooth shells with a radially striated embryophore. They contain a hexacanth embryo. The metacestode larval stage (*Coenurus cerebralis*) is readily recognised when mature as a large fluid-filled cyst up to 5 cm or more in diameter bearing random clusters of invaginated scolices, sometimes up to several hundred, on its internal wall (Fig. 1.118). The coenurus bears clusters of several hundred protoscolices on its internal wall.

Life cycle: The intermediate host is infected through the ingestion of *T. multiceps* eggs. Each egg contains an oncosphere that hatches and is activated in the small intestine. The oncosphere then penetrates the intestinal mucosa and is carried via the blood to the brain or spinal cord where each oncosphere develops into the metacestode larval stage (*Coenurus cerebralis*). In goats, the cysts can also

LIFE CYCLE 21. LIFE CYCLE OF *TAENIA HYDATIGENA*

Taenia hydatigena is a hooked cestode that, at the adult stage, lives in the small intestine of dogs, which act as definitive hosts (1). Eggs are released from the proglottids shed with the host faeces (2); following ingestion of the eggs by suitable intermediate hosts (i.e. cattle, sheep, pigs), the hexacanth larvae are released in the small intestine (3). From here, the larvae migrate via the circulation to the parenchyma of the liver (4). In the latter, the larva, known as '*Cysticercus tenuicollis*', grows into an immature vesicle (5) containing the invaginated protoscolex immersed in clear fluid. The cysticercus actively traverses the hepatic serosa and, once in the peritoneum (final site), adheres to the peritoneal serosa and completes development into a pear-shaped vesicle (up to 8 cm) with a thin and long neck; the protoscolex occurs at the neck's extremity (6). Dogs become infected by ingesting raw or undercooked offal from infected sheep or sheep carcasses abandoned on pasture. Once ingested, the protoscolices evaginate in the small intestine and develop to adult tapeworms within two months (1).



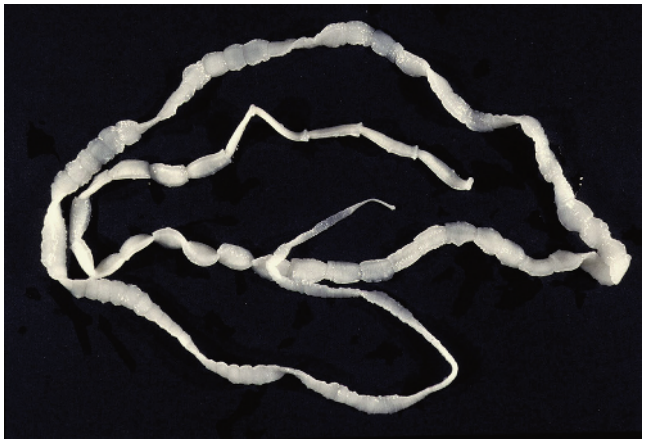


Fig. 1.116 Mature tapeworm, *Taenia multiceps*.

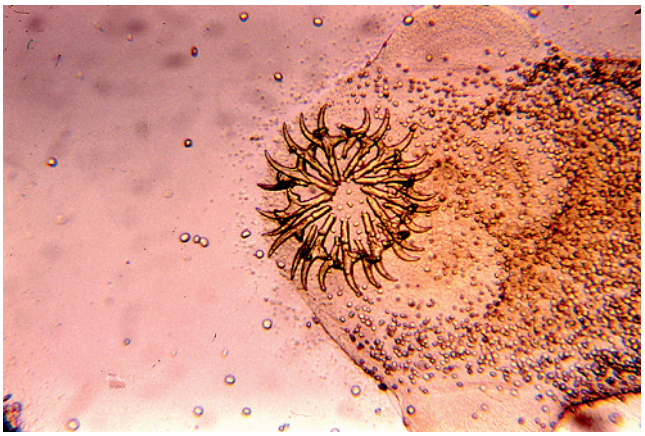


Fig. 1.117 Rostellar hooks of *Taenia* (*Multiceps*) *multiceps*.

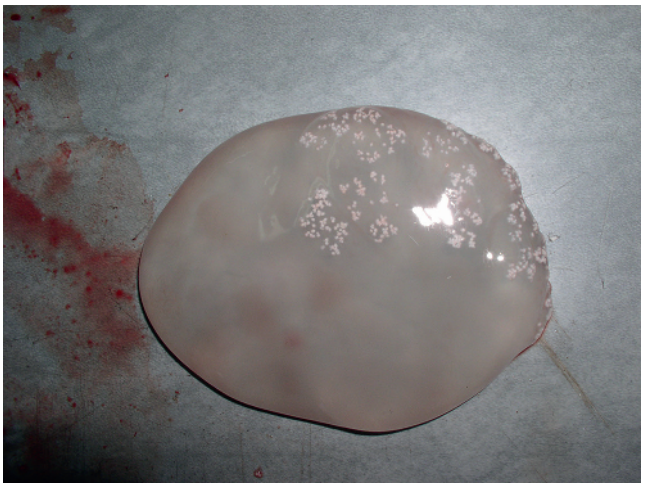


Fig. 1.118 *Coenurus cerebralis* metacestode stage of *Taenia multiceps*. (Courtesy of Andrei Mihalca).

mature in subcutaneous and intramuscular sites. The cysts in sheep and goats often persist throughout the life of the animal. The life cycle is completed when the final host, dog or wild canid, eats an infected sheep brain or spinal cord.

Taenia ovis

Synonyms: *Cysticercus ovis*, *Taenia cervi* (*Cysticercus cervi*), *Taenia krabbei* (*Cysticercus tarandi*), *Taenia hyaenae* (*Cysticercus dromedarii*, *Cysticercus cameli*)

Description: The adult tapeworm is large, measuring 0.5–1.5 m in length. The rostellum bears 24–36 hooks. The strobila has a scalloped edge and is often coiled into a spiral. The mature proglottids have a vaginal sphincter and the ovary and vagina cross each other. The uterus of the gravid proglottids has 20–25 lateral branches on either side. The oval egg measures 34 by 24–28 µm. Mature cysticerci are ovoid, white and around 3.5–10 mm and contain a single protoscolex, which is invaginated and armed with hooks and a rostellum (Fig. 1.119). In the intermediate host, each cysticercus occurs within a small cyst measuring about 4 mm or less in length.

Life cycle: Dogs and wild canids are infested by consuming the cysticercus in the intermediate host. The intermediate host is infected through the ingestion of tapeworm eggs that hatch in the intestine. The metacestode stage (*Cysticercus ovis*) infects the musculature and cysts are usually located in the skeletal muscle, heart, diaphragm and intermuscular connective tissue. The cyst becomes infective around 2–3 months after infection of the host. The prepatent period in dogs is around 6–9 weeks.

Taenia pisiformis

Synonym: *Cysticercus pisiformis*

Description: The adult tapeworm can measure up to 2 m in length. It has a large scolex with narrow strobila and the rostellum has 34–48 hooks in two rows (Fig. 1.120). Gravid segments have a uterus with 8–14 lateral branches on either side. The cysticercus is a small pea-like transparent cyst and usually occurs in bunches. Eggs are oval or elliptical, approximately 48 by 46 µm in size, and have thick smooth shells with a radially striated embryophore. They contain a hexacanth embryo.

Life cycle: Infection of the intermediate host is through ingestion of tapeworm eggs shed by dogs. Ingested eggs hatch in the small intestine of the intermediate host and penetrate the intestinal wall and pass via the portal system to the liver. Juvenile stages migrate through the liver parenchyma and locate in the abdominal cavity after 2–4 weeks, where they develop into cysts (*Cysticercus pisiformis*) attached to the wall of the mesentery and omentum. Cysts can survive the life of the host. The final host is infected by ingesting the cysticercus. The prepatent period in the dog is around 6–8 weeks.

Taenia saginata

Synonyms: *Taeniarhynchus saginata*, *Cysticercus bovis*

Description: The adult tapeworm is usually 5–8 m long, rarely up to 15 m. The scolex has neither a rostellum nor hooks. Gravid segments are 16–20 mm long by 4–7 mm wide and the uterus has

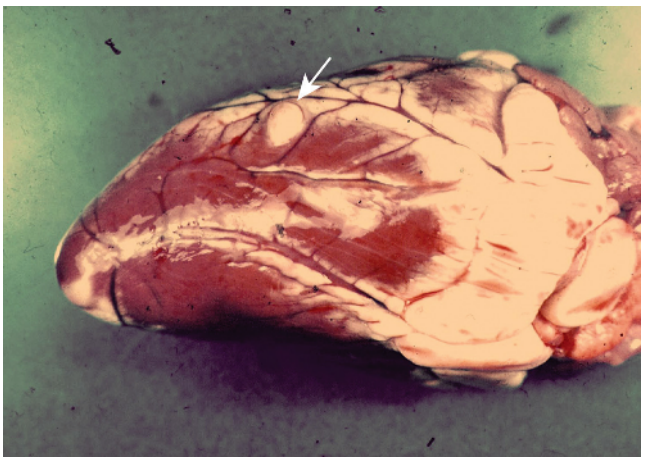


Fig. 1.119 *Cysticercus ovis* metacestode stage of *Taenia ovis* in sheep heart (arrowed).

Fig. 1.120 Scolex of *Taenia pisiformis* showing the four suckers and armed rostellum.

15–35 lateral branches on either side. In cattle, the mature cysticercus, *C. bovis*, is greyish-white, oval, about 0.5–1 by 0.5 cm long, and filled with fluid in which the scolex is usually clearly visible. As in the adult tapeworm, it has neither rostellum nor hooks.

Life cycle: An infected human may pass millions of eggs daily, either free in the faeces or as intact segments each containing about 250 000 eggs, and these can survive on pasture for several months. After ingestion by a susceptible bovine, the oncosphere travels via the blood to striated muscle. It is first grossly visible about two weeks later as a pale semi-transparent spot about 1 mm in diameter, but is not infective to humans until about 12 weeks later when it has reached its full size of around 1 cm. By then, it is enclosed by the host in a thin fibrous capsule but despite this the scolex can usually still be seen. The longevity of the cysts ranges from weeks to years. When they die, they are usually replaced by a caseous crumbly mass, which may become calcified. Both living and dead cysts are frequently present in the same carcass. Humans become infected by ingesting raw or inadequately cooked meat. Development to patency takes 2–3 months. See **life cycle 22**.

Taenia serialis

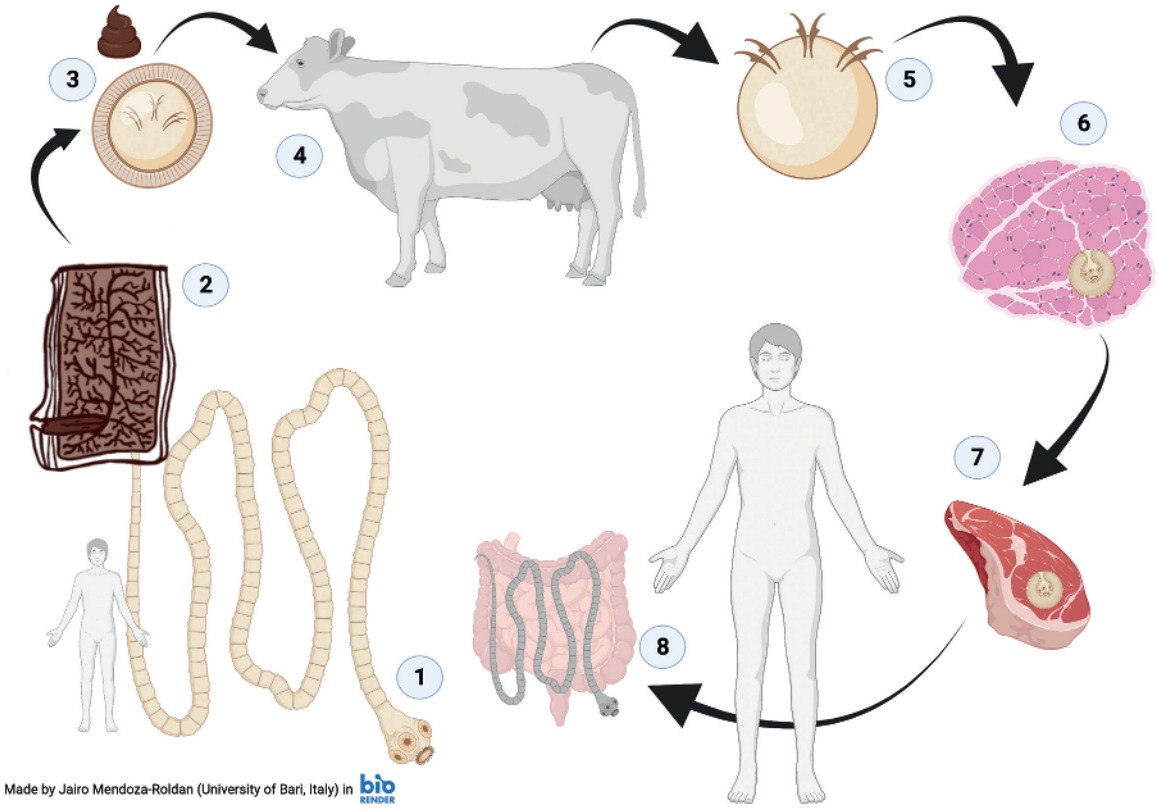
Synonyms: *Multiceps serialis*, *Coenurus serialis*

Description: The adult tapeworm is of medium length, around 0.5–0.7 m long. The scolex is armed with two rows of 26–32 hooks (Fig. 1.121). The metacestode cysts may be 4–6 cm in size and the scolices are distributed in packed rows within the cyst. The numerous scolices in the coenurus are arranged in lines or strands, as the name '*serialis*' implies. The gravid uterus has 10–18 lateral branches and the vaginal sphincter is well developed. The slightly elliptical eggs measure 31–34 by 29–30 µm and have thick smooth shells with a radially striated embryophore. They contain a hexacanth embryo.

Life cycle: Infection of the intermediate host is through ingestion of tapeworm eggs shed by dogs. The intermediate stage, *Coenurus serialis*, is found in the rabbit, usually subcutaneously or in the intermuscular connective tissue. The final host is infected by ingesting the metacestode stage.

LIFE CYCLE 22. LIFE CYCLE OF *TAENIA SAGINATA*

Taenia saginata is a harmless 8–12 meter-long cestode, found in the small intestine of humans, which act as definitive hosts (1). Each gravid proglottid features several uterus branches (15–30) and may contain up to 80 000 eggs (2). The egg contains a hexacanth larva that features three pairs of hooks (3). Cattle, which act as intermediate hosts (4), acquire the infection by ingesting eggs or gravid proglottids shed in the faeces of the human definitive hosts. In the bovine intestine, eggs hatch the oncospheres (5) that migrate via the circulation to the masseter muscle, heart, diaphragm and tongue. In these sites, the larva, known as '*Cysticercus bovis*', grows, forming a vesicle containing the invaginated protoscolex immersed in citrine fluid (6). The fully developed vesicle is elongated and measures 5 × 10 mm. Humans become infected by ingesting raw or undercooked bovine meat containing the cysticerci (7); in the intestine of the definitive host, the protoscolices evaginate and develop to adult tapeworms within 2–3 months (8).



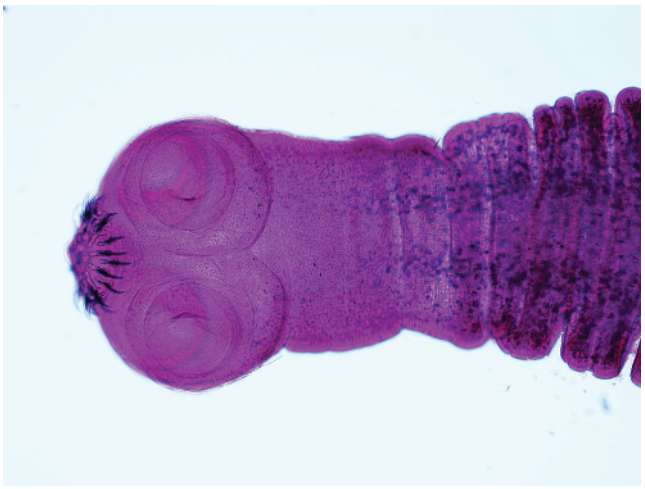


Fig. 1.121 Scolex of *Taenia serialis*.

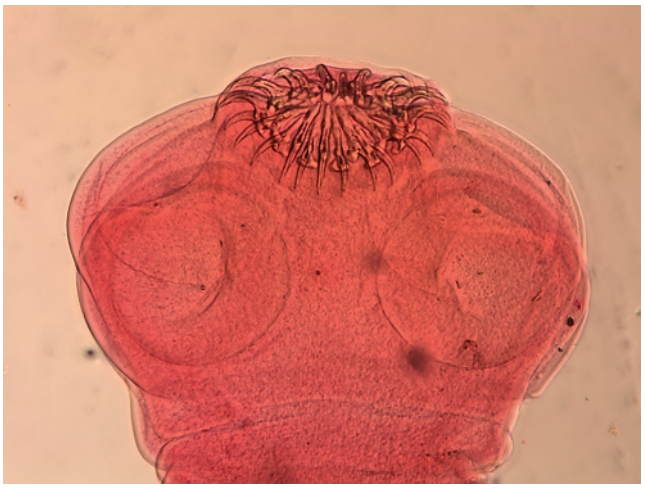


Fig. 1.122 Scolex of *Taenia solium*. (Courtesy of Libor Mikeš).

Taenia solium

Synonym: *Cysticercus solium*

Description: The adult tapeworm is 3–5 m long, rarely up to 8 m. The rostellum has four radially arranged suckers and bears four suckers and 22–32 hooks in two rows (Fig. 1.122), one row of large hooks measuring 0.14–0.18 mm and one row of smaller hooks measuring 0.11–0.14 mm. Gravid segments are 10–12 mm long and 5–6 mm wide. The ovary is in the posterior third of the proglottid and has two lobes with an accessory third lobe. The uterus has 7–12 lateral branches on either side. Adults can survive in humans for many years. Cysts are milky white and have a scolex bearing a rostellum and hooks similar to the adult. The small egg is slightly ellipsoidal with a smooth shell with a radially striated embryophore. They are yellowish-brown and measure about 35–40 by 30–35 µm and contain a hexacanth embryo. Eggs are released when the shed gravid proglottid disintegrates. The cysticerci have morphologically distinct types. The most common is the 'cellulose' cysticercus which has a fluid-filled bladder that is 0.5–1.5 cm in length with an invaginated scolex. The 'racemose' form has no evident scolex, but is larger and up to 20 cm in length.

Life cycle: Gravid segments passed in the faeces, frequently in chains, each contain around 40 000 eggs and because they are non-motile they tend to be concentrated over a small area. Eggs can also resist destruction for a relatively long period. After ingestion by a susceptible pig, the oncosphere travels via the blood to striated muscle. The principal location is the striated muscles but cysticerci may also develop in other organs, such as the lungs, liver, kidney and brain. Humans become infected by ingesting raw or inadequately cooked pork containing viable cysticerci. The human final host may also act as an intermediate host and become infected with cysticerci. This is most likely to occur from the accidental ingestion of *T. solium* eggs via unwashed hands or contaminated food. There is also, apparently, a minor route of autoinfection in a person with an adult tapeworm, from the liberation of oncospheres after the digestion of a gravid segment that has entered the stomach from the duodenum by reverse peristalsis. The prepatent period is 2–3 months. See **life cycle 23**.

Taenia taeniaeformis

Synonyms: *Hydatigera taeniaeformis*, *Taenia crassicollis*, *Strobilocercus fasciolaris*, *Strobilocercus crassicollis*

Description: The adult tapeworm is of medium size, up to 70 cm in length. The scolex is large with a double row of rostellar hooks and there is no neck region (Fig. 1.123). The uterus has 5–9 lateral branches and the posterior proglottids are bell-shaped. The metacestode stage is a strobilocercus (*Strobilocercus fasciolaris*), which is a small cyst connected with an evaginated scolex by a segmented juvenile strobila. The subspherical eggs measure on average about 31–37 µm and have thick smooth shells with a radially striated embryophore. They contain a hexacanth embryo.

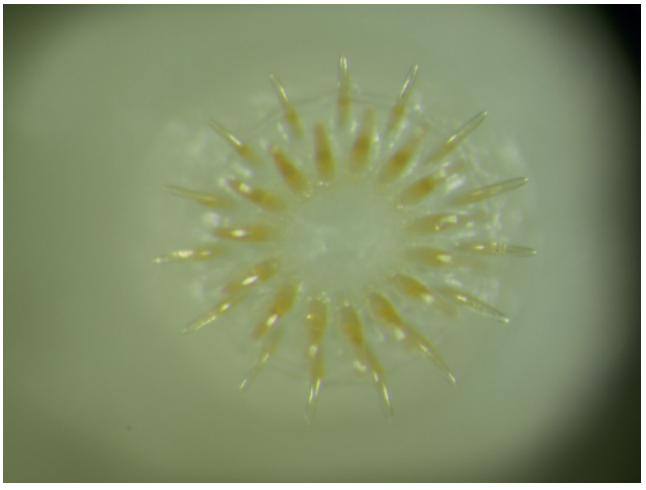
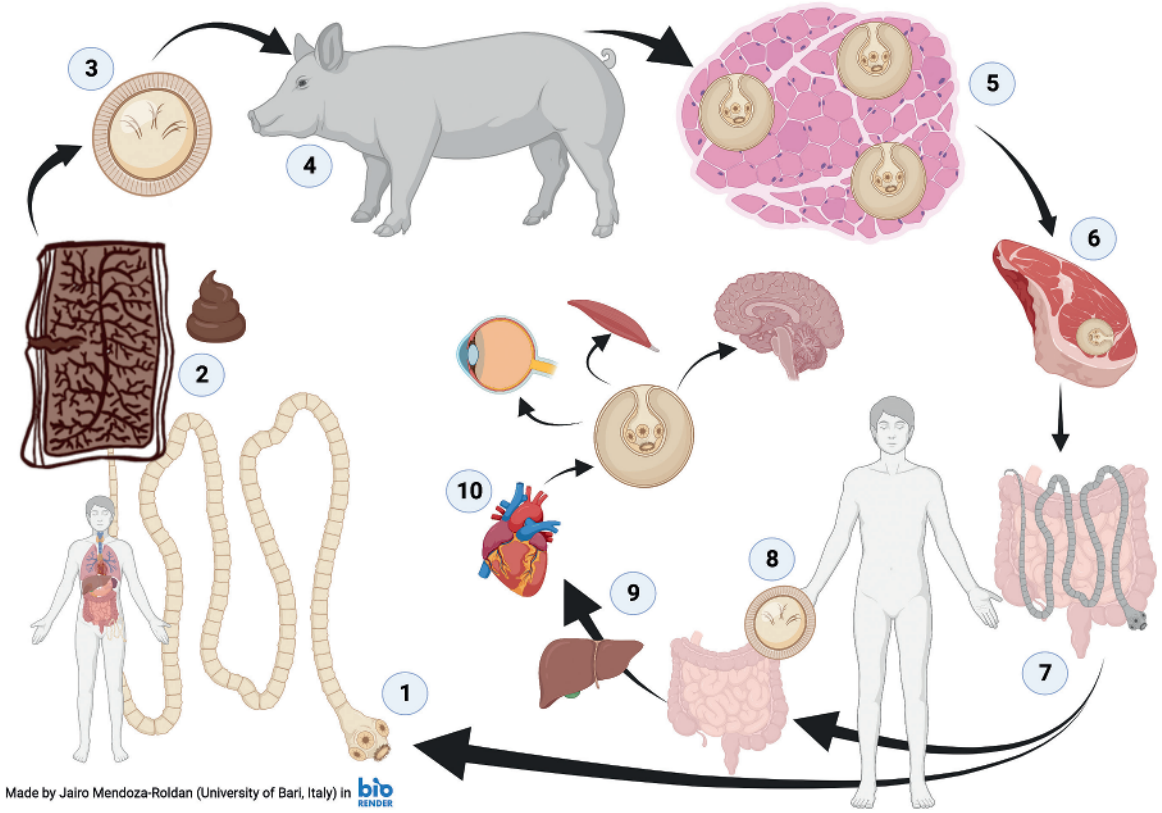


Fig. 1.123 Scolex of *Taenia taeniaeformis*. (Courtesy of Andrei Mihalca).

LIFE CYCLE 23. LIFE CYCLE OF *TAENIA SOLIUM*

Taenia solium is a 2–8 meter-long hooked cestode that, at the adult stage, is found in the small intestine of humans, which act as definitive hosts (1). The parasite's gravid proglottids are eliminated with the host faeces (2); each of these proglottids features 7–13 uterus branches and contains up to 40 000 eggs. Each egg contains a hexacanth larva, that features three pairs of hooks (3). Pigs act as intermediate hosts, which become infected by ingesting eggs or proglottids shed by infected humans (4). In the small intestine of the pig host, the eggs hatch and the oncospheres traverse the duodenal wall to invade the circulation and migrate to the skeletal muscles, particularly the masseter, tongue, heart and diaphragm (5). In these sites, the larval stage, known as '*Cysticercus cellulosae*', grow to form a whitish vesicle (20 × 10 mm) that contains the invaginated protoscolex immersed in a clear fluid (5). Humans acquire the infection by ingesting raw or undercooked pork meat containing the cysticerci (6). Once in the intestine of the definitive host, the protoscolices evaginate, attach to the intestinal mucosa (7) via the hooks and develop to adult tapeworms.

Humans can also act as accidental dead-end intermediate hosts by ingesting parasite eggs (3) or via autoinfection. If this occurs, the eggs (8) hatch in the intestine and the parasites migrate through the liver (9) and the circulatory system (10) to several organs and tissues, including skeletal muscles, eyes and central nervous system.



Life cycle: The metacestode (*Cysticercus fasciolaris*) develops in the liver of rodents and is infective to cats after about nine weeks. When a cat ingests the metacestode, the scolex attaches to the wall of the intestine. Tapeworms in cats become patent around six weeks and eggs are ingested by the intermediate host. Cats can remain infected for up to about two years.

Echinococcus

The genus *Echinococcus* is composed of several species that exploit predator–prey systems between carnivores (mainly canids) as principal hosts and intermediate hosts that range from rodents to livestock depending on the species (Table 1.58). Six species are currently recognised in the genus *Echinococcus*, with a seventh, *Echinococcus shiquicus*, recently described. Considerable phenotypic and genetic variability has been observed within the species *E. granulosus* and several strains have been identified based on molecular genotyping.

New data demonstrate that '*E. granulosus*' is an assembly of several rather diverse strains and genotypes (designated G1–G10) that show fundamental differences, not only in their epidemiology but also in their pathogenicity to humans. *Echinococcus equinus* was formerly known as the horse strain (G4) of *E. granulosus*. *Echinococcus orteleppi*, the former cattle strain (G5), is adapted to transmission by cattle. *Echinococcus oligarthus* and *E. vogeli* exist in

Table 1.58 *Echinococcus* species.

Species	Hosts	Intermediate hosts	Site
Echinococcus granulosus	Dogs, foxes, wild canids	Sheep, cattle, camels, pigs, buffalo, deer, humans	Liver, lungs
Echinococcus equinus (G4)	Dogs	Horses, donkeys	Liver
Echinococcus orteleppi (G5)	Dogs	Cattle	Liver
Echinococcus multilocularis	Dogs, foxes, cats, wild canids, humans	Rodents, pigs	Liver
Echinococcus vogeli	Wild canids	Rodents	Liver
Echinococcus oligarthus	Wild felids	Rodents	Liver

wildlife cycles and are morphologically similar to *E. multilocularis* and cause polycystic echinococcosis in humans.

Echinococcus granulosus (Echinococcus equinus, Echinococcus orteleppi)

Description: The entire cestode is only about 6 mm long, and is therefore difficult to find in the freshly opened intestine. It consists of a scolex and usually three or four segments, the terminal gravid one occupying about half the length of the complete tapeworm (Fig. 1.124). The scolex is typically taeniid and the rostellum has two rows of hooks, varying in number from 30 to 60. Each segment has a single genital opening, with the penultimate segment sexually mature and the last segment gravid. The genital pores alternate irregularly. The gravid proglottid normally disintegrates in the alimentary tract and only eggs are expelled in faeces. The small, almost spherical eggs have a smooth thick shell and are typically 'taeniid'. They measure 32–36 by 25–30 µm and the lamellar embryophore is radially striated with a six-hooked oncosphere. Hydatid cysts are large fluid-filled vesicles, 5–10 cm in diameter, with a thick concentrically laminated cuticle and an internal germinal layer. The germinal layer produces numerous small vesicles or brood capsules each containing up to 40 scolices, invaginated into their neck portions and attached to the wall by stalks. Brood capsules may become detached from the wall of the vesicle and float freely in the vesicular fluid and form 'hydatid sand'.

Life cycle: The prepatent period in the final host is around 40–50 days, after which only one gravid segment is shed per week. The oncospheres are capable of prolonged survival outside the host, being viable on the ground for about two years. After ingestion by the intermediate host, the oncosphere penetrates the gut wall and travels in the blood to the liver or in the lymph to the lungs. These are the two most common sites for larval development, but occasionally oncospheres escape into the general systemic circulation and develop in other organs and tissues. Growth of the hydatid is slow, maturity being reached in 6–12 months. In the liver and lungs, the cyst may have a diameter of up 20 cm, but in the rarer sites, such as the abdominal cavity, where unrestricted growth is possible, it may be very large and contain several litres of fluid. The cyst capsule consists of an outer membrane and an inner germinal epithelium from which, when cyst growth is almost complete, brood capsules each containing a number of scolices are budded off. Many

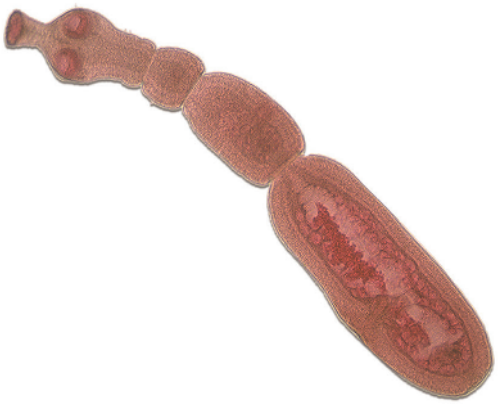


Fig. 1.124 *Echinococcus granulosus* showing the scolices and the large gravid posterior proglottids. (Courtesy of Aránzazu Meana).

of these brood capsules become detached and exist free in the hydatid fluid; collectively, these and the scolices are often referred to as 'hydatid sand'. Sometimes, complete daughter cysts are formed either inside the mother cyst or externally; in the latter case, they may be carried to other parts of the body to form new hydatids. See **life cycle 24**.

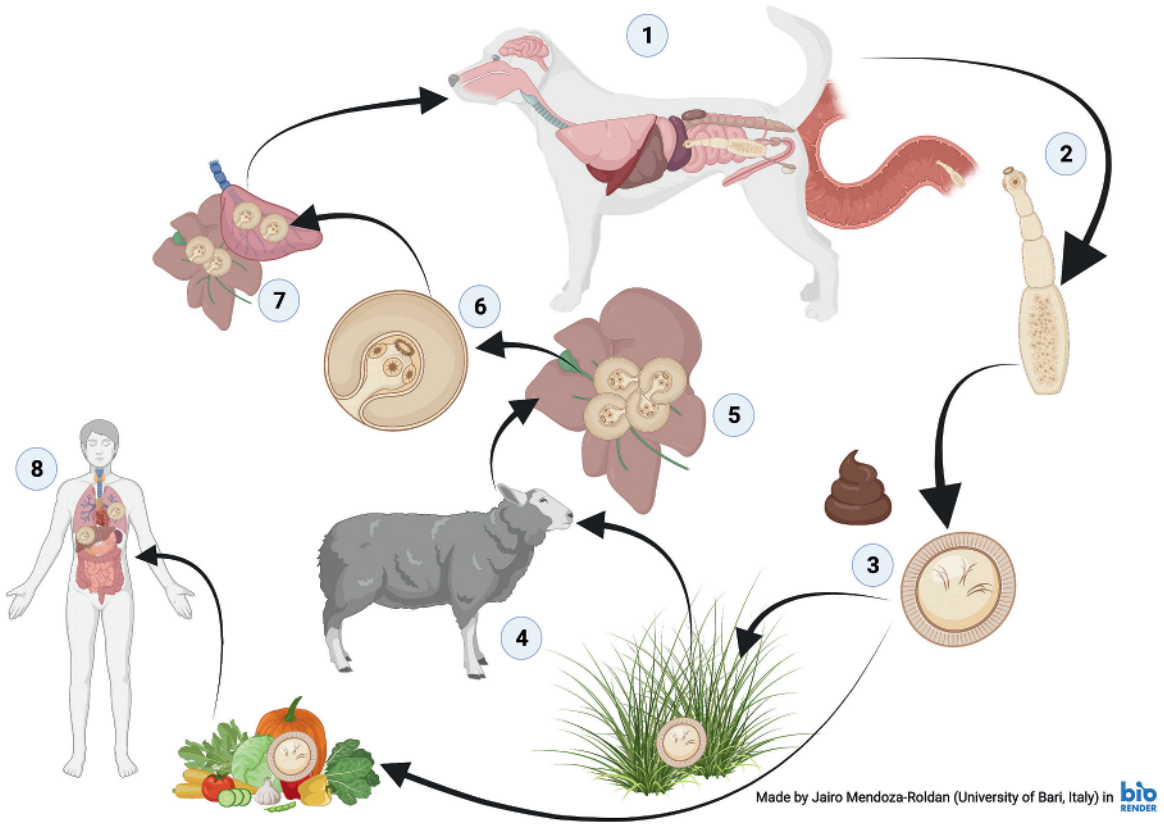
Echinococcus multilocularis

Description: *Echinococcus multilocularis* is a very small tapeworm (2–4 mm) and is generally similar to *E. granulosus*, but usually with 3–5 segments, the terminal one measuring less than half the length of the whole worm (Fig. 1.125). The scolex has four suckers and possesses a double row of large and small hooks (about 14–34). The third segment of the adult tapeworm is sexually mature and the genital pores are in front of the middle of each segment. The uterus is sac-like with no lateral sacculations in the terminal proglottid. Gravid segments contain around 200–300 spherical eggs. Eggs that are shed have a diameter of about 30–40 µm. The structure of the metacestode consists of a germinative gelatinous matrix forming a cystic structure with internal brood capsules and protoscolices

Fig. 1.125 *Echinococcus multilocularis*. (Courtesy of Libor Mikeš).

LIFE CYCLE 24. LIFE CYCLE OF *ECHINOCOCCUS GRANULOSUS*

Adult stages of *Echinococcus granulosus* (~6 mm in length) live in the small intestine of the dog, which acts as definitive host (1). The dog sheds the last proglottid of the adult tapeworm with the faeces (2); in the environment, the proglottid releases several eggs (3) that contaminate the surroundings. Depending on the genotype of *Echinococcus*, several animal species may act as intermediate hosts. The main intermediate host is the sheep (4), that acquires the infection by ingesting eggs contaminating the environment. In the sheep intestine, the eggs hatch, releasing hexacanth larvae that, via the circulation, travel to the liver (5) (where the vast majority of them establish), lungs and other organs and tissues. In these sites, the hexacanth embryos develop slowly to form cysts; these are characterised by an external capsule, a middle layer and an internal membrane, known as the 'germinative membrane'. The cysts are known as 'hydatids' and represent the larval form of the parasite (metacestode), that are also named '*Echinococcus polymorphus*' (syn. *Echinococcus granulosus*). The hydatids contain a clear fluid and several daughter and granddaughter cysts, each of which contains protoscolices (6). The life cycle is complete when a definitive host (dog) ingests infected sheep offal (7) containing the hydatids. In the small intestine of the dog, the protoscolices evaginate and, after attaching to the intestinal mucosa, develop into adult tapeworms. Humans acquire the infection by ingesting food (particularly poorly washed fruit and vegetables) contaminated with tapeworm eggs. In such an occurrence, humans act as intermediate hosts, with the parasite undergoing an identical cycle to that described for the sheep, with hydatid cysts forming in several organs and tissues, particularly liver and lungs (8).



which form racemose proliferative masses of metacestodes within infected livers of the intermediate hosts.

Life cycle: *Echinococcus multilocularis* is typically maintained in a sylvatic (wildlife) cycle, although in some rural communities a synanthropic cycle occurs with the domestic dog acting as definitive host. The intermediate host is infected by ingestion of the oncosphere and subsequent passage, via the circulatory system, to the liver where it develops into a multilocular or alveolar cyst (metacestode stage). The cycle is completed when the definitive host consumes an infected intermediate host, the mature tapeworm developing in about five weeks. Adult tapeworms are relatively short-lived, about six months.

Echinococcus vogeli

Description: *Echinococcus vogeli* is a very small tapeworm (4–6 mm) and usually has three segments, the terminal gravid segment being very long in comparison to the rest of the tapeworm. The uterus is sac-like, long and tubular in shape. The metacestode has a polycystic structure.

Echinococcus oligarthus

Description: *Echinococcus oligarthus* is an extremely small tapeworm (2.5–3 mm) and usually has three segments. The uterus is sac-like, long and tubular in shape. The metacestode has a polycystic structure.

FAMILY ANOPLOCEPHALIDAE

These are essentially tapeworms of horses (*Anoplocephala*, *Paranoplocephala*) and ruminants (*Moniezia*, *Stilesia*, *Thysanosoma*, *Thysaniezia* and *Avitellina*) (Table 1.59). Species of *Cittotaenia* are found in lagomorphs. The scolex has neither rostellum nor hooks and the gravid segments are wider than they are long. The intermediate stage is a cysticercoid present in forage mites of the family Oribatidae.

Life cycle: Mature segments are passed in the faeces and disintegrate, releasing the eggs. These are ingested by forage mites in which they develop to the cysticercoid stage in 2–4 months. The adult tapeworms are found in the intestine of horses 1–2 months after the ingestion of infected mites in the herbage.

Anoplocephala

Cestodes of this genus infect the gut of horses, donkeys and other equids, and are transmitted by Oribatidae mites.

Anoplocephala perfoliata

Description: Adult tapeworms measure 4–8 cm in length and 1.2 cm in width. There is a small rounded scolex, 2–3 mm in diameter, with a pair of 'lappets' just behind the four suckers, but there is neither rostellum nor hooks. It has a very short neck and the strobila widens rapidly, individual proglottids being much wider than they are long and containing only a single set of reproductive organs. The large gravid uterus is lobed and shaped like a sac. Eggs are irregularly spherical or triangular, 65–80 µm in diameter, and contain a hexacanth embryo. They have a thin smooth multilayered shell. The oncosphere is supported by a pair of chitinous projections, the pyriform apparatus. Gravid proglottids release the eggs as they disintegrate. Oncospheres can survive for 6–9 months in the environment unless they are frozen.

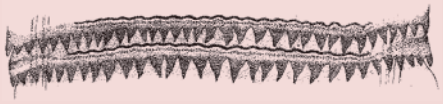
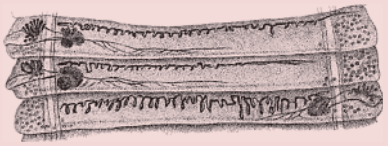
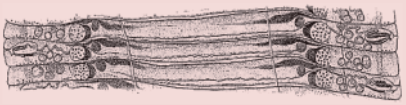
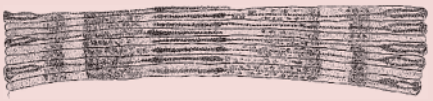
Anoplocephala magna

Description: *Anoplocephala magna* is similar morphologically to *A. perfoliata* but much longer, up to 80 cm long by 2.5 cm wide, and is similar to a broad ribbon. The scolex is large, 4–6 mm wide, with suckers opening anteriorly, and there are no lappets on the scolex. The neck is short, as are the segments. The genital organs are single and the pores are unilateral. Eggs are similar to those of *A. perfoliata* but slightly smaller and rounder, measuring 50–60 µm.

Paranoplocephala

Cestodes of this genus infect the small intestine of horses and donkeys (*Paranoplocephala mamillana*), and rabbits (*Paranoplocephala cunniculi*), and are transmitted by Oribatidae mites.

Table 1.59 Tapeworms of ruminants.

Tapeworm	Description
Moniezia	Long, wide tapeworms up to 600 cm long. Segments broader than long with two sets of genital organs
M. expansa	Row of interproglottid glands along whole breadth of posterior border 
M. benedeni	Interproglottid glands confined to short row close to the middle of the posterior margin 
Thysanosoma actinoides	Short tapeworms up to 30 cm long. Segments short and fringed posteriorly containing two sets of genital organs 
Thysaniezia ovilla	Long tapeworms up to 200 cm long. Segments wider than long with single genital pore alternating irregularly 
Stilesia globipunctata	Short thin tapeworms up to 60 cm long. Single genital pore alternating irregularly. Two distinct set of testes present 
Avitellina centripunctata	Long thin tapeworms up to 300 cm in length. Segments wider than long and indistinct except for last few. Single genital pore alternating irregularly 

Source: Drawings reproduced from Ransom (1911) and Soulsby (1971). Reproduced with permission from Lord Soulsby of Swaffham Prior.

Paranoplocephala mamillana

Synonym: *Anoplocephaloides mamillana*

Description: *Paranoplocephala mamillana* is only 10–50 mm long by 4–6 mm wide and is often referred to as the Equine 'dwarf tapeworm'. There are no lappets on the narrow scolex and the suckers are slit-like and located ventrally and dorsally. The scolex is large and without rostellum and hooks. The gravid segments are wider than they are long. Eggs are irregularly spherical or triangular and measure 51 by 37 µm in diameter.

Life cycle: Mature proglottids or eggs are passed in the faeces and on to pasture where the oncospheres are ingested by forage mites. The oncospheres are only infective for mites for about three months. The embryos migrate into the body cavity of the mite where they develop

to cysticercoids in 1–4 months and infection of the final host is by ingestion of infected mites during grazing. The prepatent period is approximately six weeks but the adult worms appear to be short-lived, patent infections persisting for only about three months.

Moniezia

Cestodes of this genus infect the small intestine of sheep, goats, cattle and buffalo, and are transmitted by Oribatidae mites.

Moniezia expansa

Description: These are long tapeworms, up to 2 m or more, which possess unarmed scolices and have four prominent suckers (Fig. 1.126). Segments are broader than they are long (up to 1.5 cm wide) and contain two sets of genital organs grossly visible along the lateral margin of each segment (Fig. 1.127; see also Table 1.59). There is a row of interproglottid glands extending along the whole breadth of the posterior border of each segment, which may be used in species differentiation. In *M. expansa* they extend along the full breadth of the segment; in *Moniezia benedeni* they occupy only the midzone of the segment. The irregularly triangular-shaped eggs have a well-defined pyriform apparatus and vary from about 50 to 67 µm in diameter (see Fig. 4.4). See **life cycle 25**.

Moniezia benedeni

Description: Grossly similar to *M. expansa*. Segments are broader than they are long (up to 2.5 cm wide). There is a row of interproglottid glands at the posterior border of each segment, which may be used in species differentiation; in *M. benedeni* they are confined to a short row close to the middle of the segment (see Table 1.59). The medium-sized irregularly quadrangular eggs have a well-defined pyriform apparatus and vary from 80 to 90 µm in diameter. The egg has a thick smooth shell and contains an embryo.

Fig. 1.126 Scolex of *Moniezia expansa* with four prominent suckers.

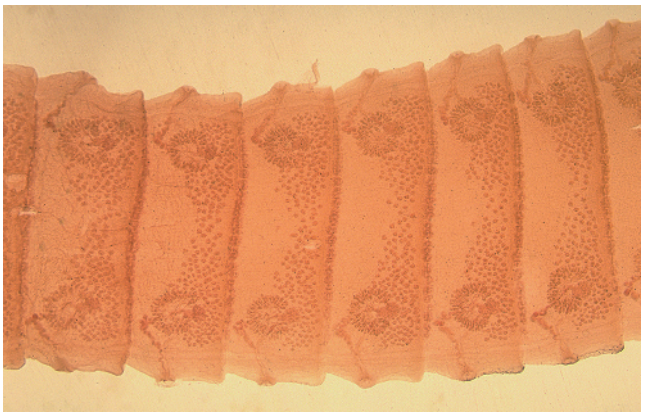


Fig. 1.127 Proglottids of *Moniezia expansa* containing two sets of genital organs. (Courtesy of Aránzazu Meana).

Thysanosoma

The main species is *Thysanosoma actinoides* which infects the small intestine, bile and pancreatic ducts of sheep, cattle and deer. This parasite has oribatid mites (*Galuma*, *Scheloribates*) and psocids (bark lice, dust lice) as intermediate hosts.

Thysanosoma actinoides

Description: The adult 'fringed' tapeworms measure 15–30 cm in length by 8 mm in width. The scolex is up to 1.5 mm in breadth; segments are short and fringed posteriorly. In the distal regions of the tapeworm, the 'fringes' are as long as the proglottid (Fig. 1.128; see also Table 1.59). Each proglottid contains two sets of genital organs with the testes lying medially. Several parauterine organs are present in each proglottid and the oval eggs (measuring about 27 × 18 µm) have no pyriform apparatus.

Life cycle: Mature segments are passed in the faeces of the infected host onto pasture, where forage mites ingest the oncospheres. Cysticercoids develop within the oribatid intermediate hosts and infection of the final host is by ingestion of infected mites during grazing.

Thysaniezia

The main species is *Thysaniezia ovilla* (syn. *Thysaniezia giardia*, *Helictometra giardi*) which infects the small intestine of cattle, sheep, goats, camels, wild ruminants and occasionally pigs. This parasite has oribatid mites (*Galuma*, *Scheloribates*) and psocids (bark lice, dust lice) as intermediate hosts.

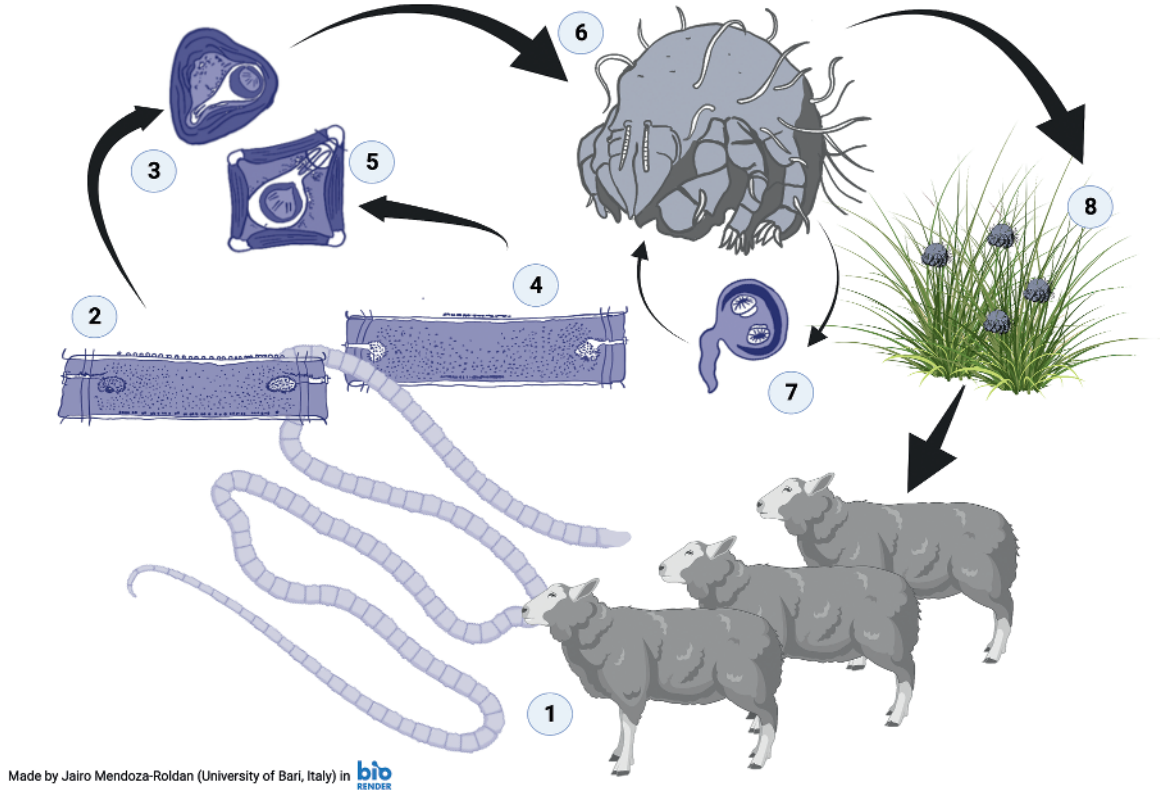
Thysaniezia ovilla

Synonyms: *Thysaniezia giardia*, *Helictometra giardi*

Description: Adults reach 200 cm in length, varying in width up to 12 mm. The scolex is small, measuring up to 1 mm in diameter. Segments are short, bulge outwards, giving the margin of the worm an irregular appearance, and contain a single set of genital organs, rarely two, with genital pores alternating irregularly (see Table 1.59).

LIFE CYCLE 25. LIFE CYCLE OF *MONIEZIA EXPANSA* AND *MONIEZIA BENEDENI*

Moniezia parasites live in the intestine of ruminants (1) and gravid proglottids are eliminated with the faeces. *Moniezia expansa* is characterised by groups of interproglottid glands that localise along the entire posterior length of each proglottid (2). The egg of *M. expansa* is hexagonal in shape, and the oncosphere is enclosed within a pear-shaped apparatus (3). In *Moniezia benedeni*, the interproglottid glands localise to the centre of the posterior side of each proglottid (4) and the eggs are rhomboid in shape (5). In the external environment, the oncospheres resume their development once ingested by oribatid mites (intermediate hosts) (6). Inside these hosts, within 1-4 months, the oncospheres develop into cysticercoid larvae (7). The life cycle is complete when infected mites are ingested by ruminant hosts (8). In these hosts, the cysticercoids develop into adult tapeworms (1) after ~6 weeks.



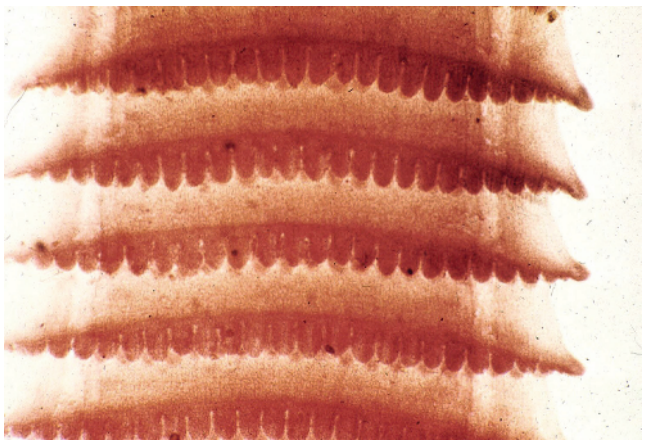


Fig. 1.128 *Thysanosoma actinoides* showing 'fringed' proglottids.

The oval eggs (measuring up to 27 by 19 µm) have no pyriform apparatus and have a thick grey shell and a protuberance at one end. They are found in groups of 10–15 in the numerous elongated parauterine organs (100 µm long) in each proglottid.

Life cycle: Mature segments are passed in the faeces of the infected host onto pasture, where forage mites ingest the oncospheres. Cysticercoids develop within the oribatid intermediate hosts and infection of the final host is by ingestion of infected mites during grazing.

Stilesia

Cestodes of this genus infect the guts and liver of several ruminants (Table 1.60).

Table 1.60 *Stilesia* species.

Species	Hosts	Site	Intermediate hosts
Stilesia globipunctata	Sheep, goats, cattle, other ruminants	Small intestine	Oribatid mites and psocid lice
Stilesia hepatica	Sheep, goats, cattle, wild ruminants	Liver, bile ducts	Oribatid mites?
Stilesia vittata	Camels	Small intestine	Oribatid mites?

Stilesia globipunctata

Description: Adults measure 45–60 cm in length by 3–4 mm in width. The narrow scolex has four large suckers but no hooks. Strobila is broader than long. A single set of genital organs is present and genital pores alternate irregularly (see Table 1.59). Two distinct sets of testes are present in each segment, one on each side, but no testes in the median line. Eggs lack a pyriform apparatus and measure around 27 by 15 µm. See **life cycle 26**.

Stilesia hepatica

Description: The adult tapeworm measures 20–50 cm in length and 2–3 mm in width. The neck is narrow and the scolex is large with prominent suckers. The genital organs are single and the opening pores alternate irregularly. There are 10–12 testes on either side lying dorsal to the ventral canal. The proglottids are short. The oval eggs lack a pyriform apparatus and measure about 26–30 by 16–19 µm.

Life cycle: The life cycle is not known but probably involves oribatid mites.

Stilesia vittata

Description: Adults are 18–23 cm long. Mature proglottids contain 5–7 testes lying lateral to the ventral canal.

Avitellina

Species of this genus occur in the small intestine of ruminants in parts of Africa, Europe and India (Table 1.61).

Life cycle: The life cycle is similar to that of *Moniezia*.

Avitellina centripunctata

Synonym: *Avitellina woodlandi*

LIFE CYCLE 26. LIFE CYCLE OF *STILESIA HEPATICA* AND *STILESIA GLOBIPUNCTATA*

Stilesia globipunctata and *Stilesia hepatica* are harmless cestodes (up to 50 cm in length) that, in the adult stage (1), live in the small intestine (2) and the biliary ducts (3), respectively, of small ruminants (definitive hosts). The proglottids are wider than long and feature irregularly distributed genital pores. The ovoid-shaped eggs contain an oncosphere with a pear-shaped apparatus (4). Once excreted into the environment with the host's faeces, the eggs are ingested by coprophagic oribatid mites (*Scheloribates* spp., 5), which act as intermediate hosts. Inside the mite, the oncosphere develops into a cysticercoid (6). Small ruminants become infected while grazing on pastures contaminated with mites containing the cysticercoids (7); once in the small intestine of the definitive host (8), the cysticercoids evaginate and develop to adult tapeworms (1).

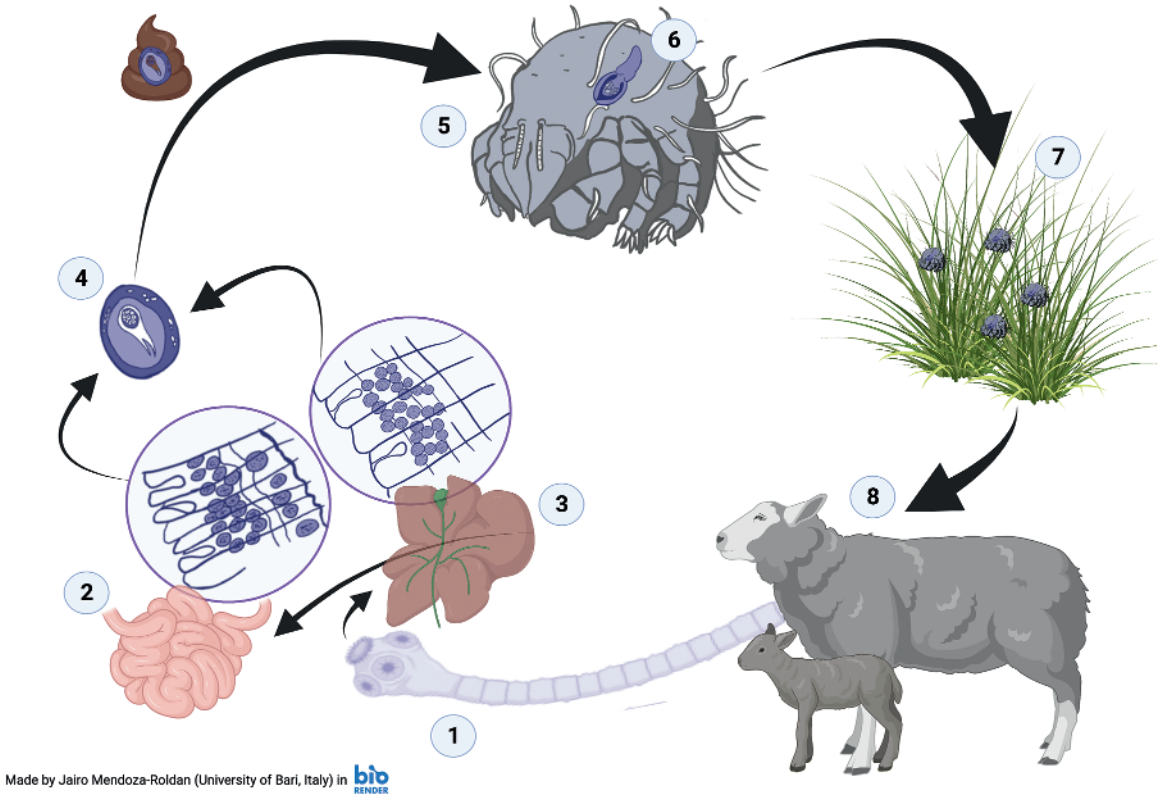


Table 1.61 *Avitellina* species.

Species	Hosts	Site	Intermediate hosts
Avitellina centripunctata (syn. *Avitellina woodlandi*)	Sheep, goats, camels and other ruminants	Small intestine	Oribatid mites or psocid lice
Avitellina goughi	Sheep	Small intestine	Oribatid mites or psocid lice
Avitellina chalmersi	Sheep	Small intestine	Oribatid mites or psocid lice
Avitellina tatia	Goats	Small intestine	Oribatid mites or psocid lice

Description: This tapeworm resembles *Moniezia* on gross inspection except that the segmentation is so poorly marked that it appears somewhat ribbon-like. It can reach 3 m in length and about 3–4 mm in width and the posterior end is almost cylindrical in appearance. Proglottids are short with indistinct segmentation and single genitalia present with the pores alternating irregularly (see Table 1.59). Eggs lack a pyriform apparatus and measure around 20–45 µm. They are contained in capsules in a single parauterine organ in each proglottid.

Cittotaenia

Parasites of this genus are found in rabbits and hares (Table 1.62).

Life cycle: Mature proglottids or eggs are passed in the faeces and onto pasture where the oncospheres are ingested by forage mites. The embryos migrate into the body cavity of the mite where they develop to cysticercoids. Infection of the final host is by ingestion of infected mites during grazing.

Cittotaenia ctenoides

Description: Mature tapeworms grow up to 80 cm long and 1 cm wide. The scolex is about 0.5 mm wide and bears a short neck. The proglottids are much wider than they are long and each contains two sets of genital organs containing 60–80 testes behind an ovary on each side.

Cittotaenia denticulata

Description: Differs from *C. ctenoides* by having a wider scolex (0.8 mm) and no neck.

Cittotaenia pectinata

Description: Very similar to *C. ctenoides* but with a smaller scolex (0.25 mm) but also bears a short neck.

Table 1.62 *Cittotaenia* species.

Species	Hosts	Site	Intermediate hosts
Cittotaenia ctenoides	Rabbits	Small intestine	Oribatid mites
Cittotaenia denticulata	Rabbits	Small intestine	Oribatid mites
Cittotaenia pectinata	Rabbits, hares	Small intestine	Oribatid mites

FAMILY DIPYLIDIIDAE

These are small to medium-sized tapeworms of the dog and cat (*Dipylidium*, *Diplopylidium*, *Joyeuxiella*). The scolex usually has an armed rostellum with several rows of hooks. The suckers may also possess fine hooks. The gravid uterus is retained as a transverse sac. The intermediate stage is a cysticercoid.

Dipylidium

This is the most common tapeworm genus of the domestic dog and cat. *Dipylidium* is a much shorter tapeworm than *Taenia*, the maximum length being about 50 cm.

Life cycle: The newly passed segments are active, and can crawl about on the tail region of the animal. The oncospheres are contained in egg packets or capsules, each with about 20 eggs, and these are either expelled by the active segment or released by its disintegration. After ingestion by the intermediate host, the oncospheres travel to the abdominal cavity where they develop into cysticercoids. All stages of the biting louse can ingest oncospheres but the adult flea, with its mouthparts adapted for piercing, cannot do so and infection is only acquired during the larval stage, which has chewing mouthparts. Development in the louse, which is permanently parasitic and therefore enjoys a warm habitat, takes about 30 days but in the flea larva and the developing adult in the cocoon, both of which are on the ground, development may extend over several months. The final host is infected by ingestion of the flea or louse containing the cysticercoids, usually while grooming. Development to patency, when the first gravid segments are shed, takes about three weeks. The main species is *Dipylidium caninum* which infects the small intestine of dogs, foxes, cats and rarely humans. This parasite has fleas (*Ctenocephalides* spp., *Pulex irritans*) and lice (*Trichodectes canis*) as intermediate hosts. See **life cycle 27**.

Dipylidium caninum

Description: *Dipylidium* is a much shorter tapeworm than *Taenia*, the maximum length being about 50 cm. The scolex has four suckers and a protrusible retractable rostellum, which is armed with four or five rows of small rose thorn-shaped hooks (Fig. 1.129). The proglottid is easily recognised, being elongate, like a large rice grain or cucumber seed, and has two sets of genital organs, with a pore opening on each margin (Fig. 1.130). Eggs are yellowish-brown in colour and almost spherical. They contain a hexacanth embryo and measure about 25–50 µm and are contained in an egg capsule (about 120–200 µm), which may hold up to 30 eggs (Fig. 1.131; see also Fig. 4.7).

Amoebotaenia

Small tapeworms found in the duodenum of chickens, with earthworms as intermediate hosts.

Life cycle: See *Raillietina cesticillus*. The prepatent period is around 4–5 weeks. The main species is *Amoebotaenia sphenoides* (syn. *Amoebotaenia cuneata*) which infects the small intestine of chickens. This parasite has earthworms as intermediate hosts.

LIFE CYCLE 27. LIFE CYCLE OF *DIPYLIDIUM CANINUM*

Dipylidium caninum is a hooked cestode (1), up to 90 cm in length, that lives in the small intestine of companion animals (dogs and cats) (2), which act as definitive hosts. The gravid proglottids containing egg capsules detach from the strobila (3) and are eliminated with the faeces. Once in the environment, the external wall of the proglottid disintegrates, thus releasing eggs (4) contained in egg capsules (5); these are ingested by flea larvae (6), in which development of cysticercoids takes place. The development of the cysticercoids (7, 8) occurs simultaneously to that of the flea, and terminates once the flea has reached the adult stage. The definitive hosts become infected by ingesting fleas containing the cysticercoids (9); in the small intestine of these hosts, the cysticercoids mature to adult tapeworms that attach to the intestinal mucosa via the rostellum and suckers (1). Some species of lice can also act as intermediate hosts. Humans, and children in particular, may acquire the infection by ingesting fleas or lice containing the cysticercoids.

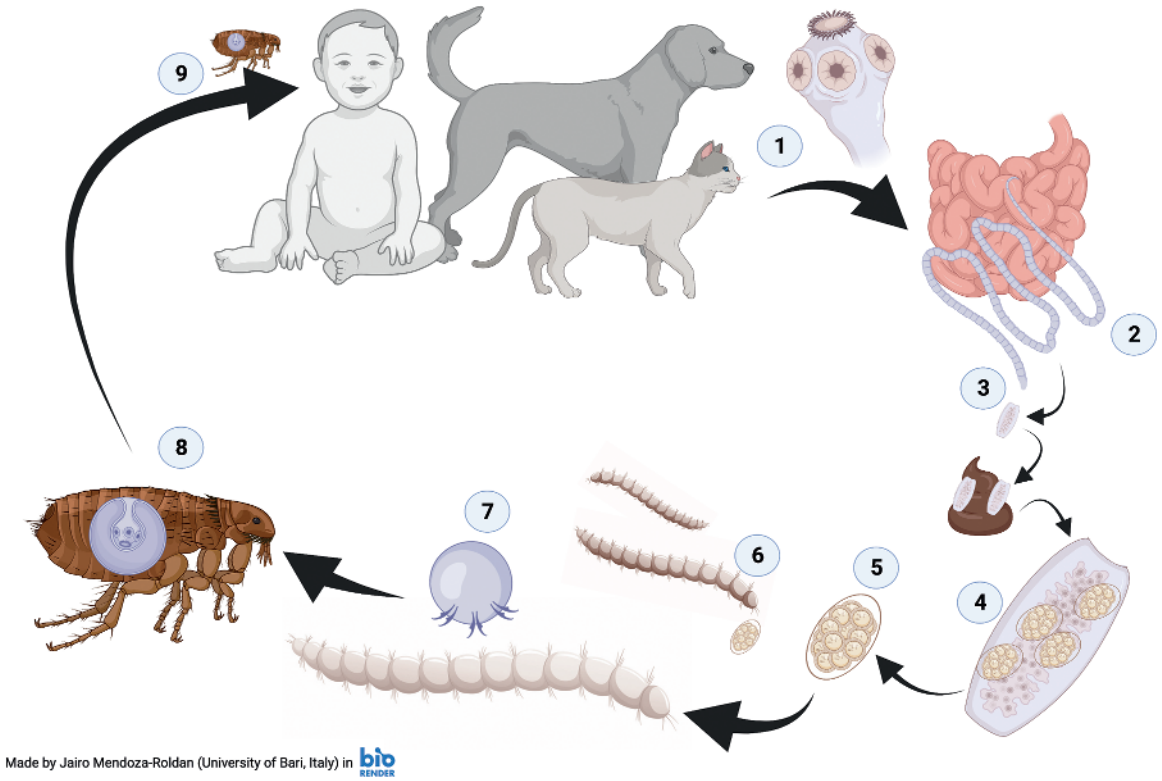


Fig. 1.129 Scolex of *Dipylidium caninum* with four suckers and protrusible rostellum.

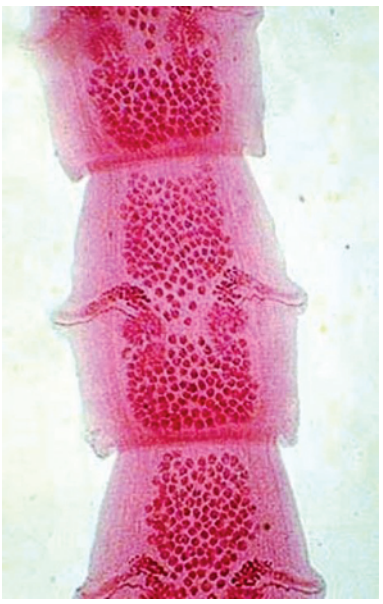


Fig. 1.130 Proglottids of *Dipylidium caninum* with two sets of genital organs.

Fig. 1.131 *Dipylidium caninum* egg packet.

FAMILY DILEPIDIDAE

Amoebotaenia sphenoides

Synonym: *Amoebotaenia cuneata*

Description: A very small tapeworm, up to about 4 mm long by 1 mm wide, with up to 20 proglottids, each wider than long. These proglottids are approximately triangular in shape, although the last few segments decrease in size. Its overall appearance is slightly fluke-like. The rostellum bears a single circular row of 12–14 hooks. In the single reproductive organ, the genital pores alternate regularly.

Choanotaenia

These are large robust tapeworms, up to 20 cm in length, found in chickens, turkeys and other gallinaceous birds. The main species is *Choanotaenia infundibulum* which infects the small intestine of chickens, turkeys and gamebirds. This parasite has house fly (*Musca domestica*), beetles (*Aphodius*, *Calathus*, *Geotrupes*, *Tribolium*) and grasshoppers as intermediate hosts.

Choanotaenia infundibulum

Description: A relatively large tapeworm up to 20 cm in length and 1.5–3 mm in width. Each segment is wider posteriorly, giving the margin of the tapeworm a 'saw-edge' appearance. The scolex is triangular, pointed anteriorly with a distinctive rostellum, ringed with about 18 slender hooks. A single set of reproductive organs is present in each proglottid and the genital pores alternate regularly.

Joyeuxiella and Diplopylidium

These two genera contain a couple of species of restricted veterinary importance. In these tapeworms, the genital apertures are sited anterior to the middle of the proglottid. Each egg capsule contains only one egg. *Joyeuxiella pasquale* has been found in the cat and the dog in Africa, the Middle East and Australia. It is very similar to *Dipylidium*. It requires two intermediate hosts: first, various beetles and second, a lizard or small mammals. *Diplopylidium nolleri* and *D. trinchesi* occur in the cat and dog in the Middle East. Two intermediate hosts are involved: first, various beetles and second, a reptile or small mammal.

FAMILY PARUTERINIDAE

Members of this family, which are parasites of birds, are closely related to the Dilepididae but possess a parauterine organ.

Metroliasthes

The main species is *Metroliasthes lucida* (syn. *Hexaparuterins lucida*) which infects the small intestine of turkeys and chickens. This parasite has grasshoppers (*Chorthippus*, *Paroxya*, *Melanopus*) as intermediate hosts.

Metroliasthes lucida

Synonym: *Hexaparuterins lucida*

Description: The tapeworm is about 20 cm long and 1.5–2 mm wide. The scolex has no rostellum or hooks and the suckers are devoid of spines. The single genital pores are irregularly alternating and can be prominent. Each gravid proglottid possesses a single parauterine organ containing one egg.

FAMILY DAVAINEIDAE

These are mainly parasites of birds (*Davainea*, *Raillietina*, *Cotugnia*, *Houttuynia*). These tapeworms usually have rows of hooks on both rostellum and suckers. Egg capsules replace the uterus in this family. The intermediate stage is a cysticercoid.

Davainea

This genus contains *Davainea proglottina*, the most pathogenic cestode of poultry.

Life cycle: Gravid proglottids are shed in faeces and eggs are ingested by various gastropod molluscs, in which they develop to the cysticercoid stage after about three weeks. Following ingestion of the mollusc by the final host, the cysticercoids develop into adult tapeworms in about two weeks. The main species is *Davainea proglottina* which infects the small intestine of turkeys, chickens, pigeons and other gallinaceous birds. This parasite has slugs (*Agriolimax*, *Arion*, *Cepaea* and *Limax*) and land snails as intermediate hosts.

Davainea proglottina

Description: *Davainea proglottina* is an extremely small cestode up to 1–4 mm long, and usually possesses only 4–9 segments (Fig. 1.132). The rostellum bears 80–94 hooks, arranged in a double

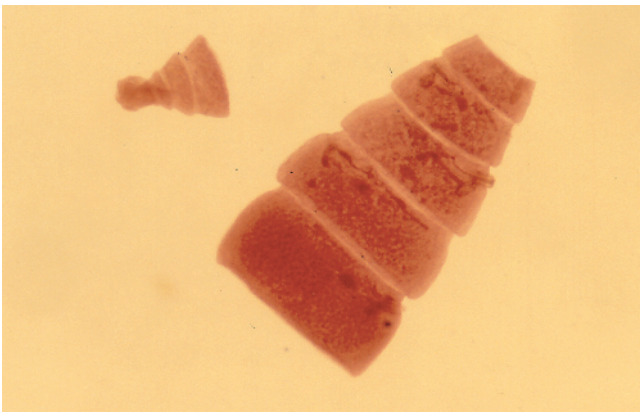


Fig. 1.132 *Davainea proglottina*: scolex and proglottids.

row, and the suckers bear a few rows of small hooks. Each segment contains a single set of reproductive organs. The genital pores alternate regularly. Eggs are spherical and measure about 30–40 µm and are found singly within the parenchymatous capsules in the gravid segment.

Raillietina

Species of this genus are found in the small intestine of chickens and turkeys and other fowl with the cysticercoid intermediate stage, depending on the species, in ants or beetles (Table 1.63).

Life cycle: Gravid proglottids are passed in faeces and eggs are ingested by various intermediate hosts. The embryo hatches from the egg in the intestine and then changes into a cysticercoid in the body cavity. Following ingestion by the final host, the activated cysticercoid attaches to the mucosa of the anterior or mid small intestine. The prepatent period is around 2–3 weeks.

Raillietina cesticillus

Description: A small tapeworm that can reach around 10–14 cm in length, but is often much shorter at about 4–5 cm long. The broad scolex is large and the rostellum wide. The unarmed suckers are not prominent and the rostellum is armed with several hundred small hammer-shaped hooks arranged in a double row. The gravid proglottids contain several thin-walled egg capsules, each housing a single egg. Eggs are spherical to slightly ellipsoidal and measure approximately 75 by 90 µm. They have a thick smooth shell and contain a hexacanth embryo (see Fig. 4.8). Eggs are shed only after the gravid proglottid or the egg capsule disintegrates.

Table 1.63 *Raillietina* species.

Species	Hosts	Site	Intermediate hosts
Raillietina cesticillus (syn. *Skrjabinia cesticillus*)	Chickens, turkeys, guinea fowl	Small intestine	Various genera of beetles, cockroaches, *Musca domestica*
Raillietina echinobothrida	Chickens, turkeys	Small intestine	Ants of the genera *Pheidole* and *Tetramorium*
Raillietina tetragona	Chickens, guinea fowl, peafowl and pigeons	Small intestine	Houseflies (*Musca domestica*) and ants of the genera *Pheidole*, *Tetramorium* and *Onthophagus*
Raillietina georgiensis	Turkeys	Small intestine	Ants of the genera *Pheidole* and *Tetramorium*

Raillietina echinobothrida

Description: *Raillietina echinobothrida*, which may be up to 25 cm in length, is similar in shape to *R. tetragona*. The suckers are circular and armed with several rows of small hooklets and the rostellum is well endowed with two rows of around 200 hooks (these features distinguish it from *R. tetragona*). A 'neck' is absent behind the scolex. The gravid proglottids contain multiple fibrous-walled egg capsules, each housing several eggs (around 6–12). Eggs are identical to those of *R. cesticillus* and measure approximately 75 by 95 µm.

Raillietina tetragona

Description: Often the largest tapeworm of fowl, reaching around 20–25 cm in length. The scolex is smaller than that of *R. echinobothrida* and the 'neck' is quite prominent. The oval suckers are lightly armed with several rows of fine hooklets and the rostellum bears one or sometimes two rows of around 100 hooks. The gravid proglottids contain multiple fibrous-walled egg capsules, each housing many eggs (about 8–14). Eggs measure approximately 50 by 25 µm. *Raillietina tetragona* has a larger number of egg capsules in the gravid proglottid than either *R. cesticillus* or *R. echinobothrida*.

Raillietina georgiensis

Description: The length of this tapeworm is around 15–35 cm. The rostellum is covered with about 100 hooks.

Cotugnia

Parasites of this genus infect the small intestine of birds (Table 1.64).

Cotugnia digonopora

Description: The tapeworm is up to 10 cm long. The head is large with a small rudimentary retractile rostellum, which is armed with two rows of small hooklets. The suckers are large and unarmed and the proglottids are wider than long. Segments possess a double set of genital organs.

Life cycle: The life cycle is unknown but is thought to involve ants or beetles.

Table 1.64 *Cotugnia* species.

Species	Hosts	Site	Intermediate hosts
Cotugnia digonopora	Chickens	Small intestine	Ants, beetles?
Cotugnia fastigata	Ducks, geese	Small intestine	Unknown
Cotugnia cuneata	Pigeons	Small intestine	Unknown

Houttuynia

The main species is *Houttuynia struthionis* which infects the small intestine of ostriches and rheas. The intermediate hosts of this parasite are unknown.

Houttuynia struthionis

Description: These are large, long, flat, white segmented tapeworms (60–120 cm long by 9 mm wide). The scolex is 1–2 mm wide and bears a double row of about 160 large and small hooks. The eggs are contained within parenchymatous capsules in the gravid proglottid. There are around 15–25 eggs in each capsule. Genital pores are unilateral.

Life cycle: The life cycle is unknown.

FAMILY HYMENOLEPIDIDAE

These small to medium-sized parasites are of minor veterinary importance. Members of this family, which have a characteristically slender strobila with a conical rostellum, infect birds, humans and rodents (*Hymenolepis*, *Rodentolepis*, *Fimbriaria*). The intermediate stage is a cysticercoid present in an arthropod host.

Hymenolepis

This genus contains a large number of species that are usually narrow and thread-like in appearance with three testes in each segment (Table 1.65).

Hymenolepis cantaniana

Synonym: *Stephylepis cantaniana*

Description: A slender tapeworm, reaching a length of up to 2 cm. The rostellum is rudimentary and the suckers are unarmed.

Table 1.65 *Hymenolepis* species.

Species	Hosts	Site	Intermediate hosts
Hymenolepis cantaniana (syn. *Stephylepis cantaniana*)	Chickens, turkeys, pheasants, quails and other fowl	Small intestine	Beetles (Scarabeidae)
Hymenolepis carioca (syn. *Echinolepis carioca*) Small intestine	Chickens, turkeys and other fowl	Small intestine	Dung and flour beetles; occasionally *Stomoxys* spp.
Hymenolepis lanceolata (syn. *Drepanidotaenia lanceolatum*)	Ducks, geese	Small intestine	Freshwater crustaceans (copepods)
Hymenolepis nana (syn. *Rodentolepis nana*, *Rodentolepis fraterna*, *Vampirolepis nana*)	Rats, mice, humans	Small intestine	Flour beetles (*Tenebrio*) or fleas
Hymenolepis diminuta (syn. *Rodentolepis diminuta*)	Rats, mice, humans	Small intestine	Moths, cockroaches, fleas, beetles, millipedes

Hymenolepis carioca

Synonym: *Echinolepis carioca*

Description: This is a slender thread-like tapeworm reaching a length of up to 8 cm. The scolex is unarmed. The proglottids number 500–1100 and are broader than they are long.

Hymenolepis lanceolata

Synonym: *Drepanidotaenia lanceolatum*

Description: A slender tapeworm reaching up to 15–20 cm in length. The proglottids are much wider than they are long.

Hymenolepis nana

Synonyms: *Rodentolepis nana*, *Rodentolepis fraterna*, *Vampirolepis nana*

Description: The tapeworm is small, 2.5–4 cm in length, and has a characteristically slender strobila with about 200 segments. The scolex has four suckers and is armed with a retractable rostellum bearing a single row of 20–30 hooks. The genitalia are single and the segments are wider than they are long. Eggs are small, round or oval in shape and measure 44–62 by 30–55 µm. They are colourless with a smooth shell and contain a lemon-shaped embryophore with protruding polar plugs that bear long fine undulated filaments. The embryo has three pairs of small hooks.

Life cycle: The life cycle can be direct, the cysticercoids developing in the villi of the small intestine of the final host and then emerging to develop to the adult tapeworm in the intestinal lumen. Otherwise, flour beetles or fleas can serve as intermediate hosts.

Hymenolepis diminuta

Synonym: *Rodentolepis diminuta*

Description: A small tapeworm, about 20–60 mm in length. The rostellum does not possess hooks. The eggs are larger than those of *R. nana*, measuring about 60 µm, and the outer membrane is darker and may be striated.

Fimbriaria

The main species is *Fimbriaria fasciolaris* which infects the small intestine of chickens, ducks, geese and wild anseriform birds. This parasite has copepods (*Cyclops* spp. and *Diaptomus* spp.) as intermediate hosts.

Fimbriaria fasciolaris

Description: This is not a common cestode. The adult tapeworms vary in length from 2.5 cm up to about 40 cm. The scolex is small with 10 hooks but the anterior part of the body possesses a 'pseudoscolex' (a folded body expansion) for attachment to the

host. The presence of this expansion aids diagnosis. The uterus is a continuous tube which separates into small tubules in the posterior of the worm. These tubules contain eggs which retain the outer spindle-shaped shell and they contain the oval embryophores. The genital pores are unilateral with three testes to each set of genital organs.

FAMILY MESOCESTOIDIDAE

Also of minor veterinary importance, these cestodes of carnivorous animals and birds have two metacestode stages. The first is a cysticercoid in an insect or mite, and the second a solid larval form, a tetrathyridium, in a vertebrate. Genera include *Mesocestoides* found in dogs, cats and wild mammals, and *Dithyridium* in chickens, turkeys and wild birds.

Mesocestoides

Adult tapeworms are found in the small intestine of dogs, cats and wild carnivores. The second intermediate stages (tetrathyridia) occur in the peritoneal and pleural cavities or subcutaneous tissue of a wide variety of vertebrate hosts (*Dithyridium*, *Tetrathyridium*).

Life cycle: The life cycle requires two intermediate hosts. A cysticercoid is produced in the first intermediate host which, when eaten by the second intermediate host, forms a tetrathyridium; this may remain as an encapsulated form for some time. The tetrathyridium is located in the peritoneal cavity in reptiles and mammals and in the lungs in birds. Dogs and cats can start to shed tapeworm segments in faeces as early as three weeks after infection. The main species is *Mesocestoides lineatus* which infects the small intestine of dogs, cats, foxes, mink, wild carnivores and occasionally humans. This parasite has oribatid mites (cysticercoid), coprophagus beetles, birds, amphibians, reptiles and mammals (tetrathyridium) as intermediate hosts.

Mesocestoides lineatus

Synonyms: *Dithyridium variable*, *Tetrathyridium bailetti*, *Tetrathyridium elongatum*

Description: The adult tapeworm ranges from 30 to 250 cm in length and up to 3 mm wide. The scolex is large, unarmed and without a rostellum, and the four suckers are elongate and oval. The strobila is thin and narrow, up to 1.5 cm in length. Mature segments are longer than wide and each contains a single set of central reproductive organs, the central genital pore opening on the dorsal surface (Fig. 1.133). The ovary and vitelline glands are bilobed and there are numerous testes. Oncospheres in gravid segments progress from the uterus into a parauterine organ. Eggs accumulate in the parauterine organ as the segments mature. The eggs are oval and measure 40–60 by 35–43 µm.

Fig. 1.133 Proglottid of *Mesocestoides lineatus* with a single set of central genital organs opening dorsally.

ORDER DIPHYLLOBOTHRIIDEA

The morphology of the Diphyllobothriidea is generally similar to that of the Cyclophyllidea, but there are three distinct features. First, the unarmed scolex has no suckers and instead has two weakly muscular, shallow longitudinal grooves or **bothria**, which become flattened to form organs of attachment. Second, the proglottids possess a uterine pore that enables eggs to be discharged from a large length of the strobila. The terminal proglottids are not gravid and usually are exhausted and may become detatched in short chains. Third, the eggshell is thick, brownish-yellow and operculate, and the **coracidium**, which emerges after hatching, is an oncosphere with an embryophore which is ciliated for mobility in water.

The pseudophyllidean life cycle utilises two intermediate hosts. The coracidium must first be ingested by a crustacean in whose body cavity a larval procercoid develops. Subsequently, if the crustacean is eaten by a freshwater fish, amphibian or reptile, the procercoid is liberated and in the muscles of the new host develops into a second larval stage, a plerocercoid, which possesses the characteristic scolex; it is only this stage which is infective to the final host.

This order contains only two genera of veterinary importance: *Diphyllobothrium* and *Spirometra*.

FAMILY DIPHYLLOBOTHRIIDAE

Parasites of cetaceans, fish-eating mammals and other vertebrates with well-developed bothria.

Diphyllobothrium

The genus *Diphyllobothrium* is an important cestode of humans and fish-eating mammals, such as dogs, cats, pigs and polar bears. They are long tapeworms with an unarmed scolex, with two muscular bothria.

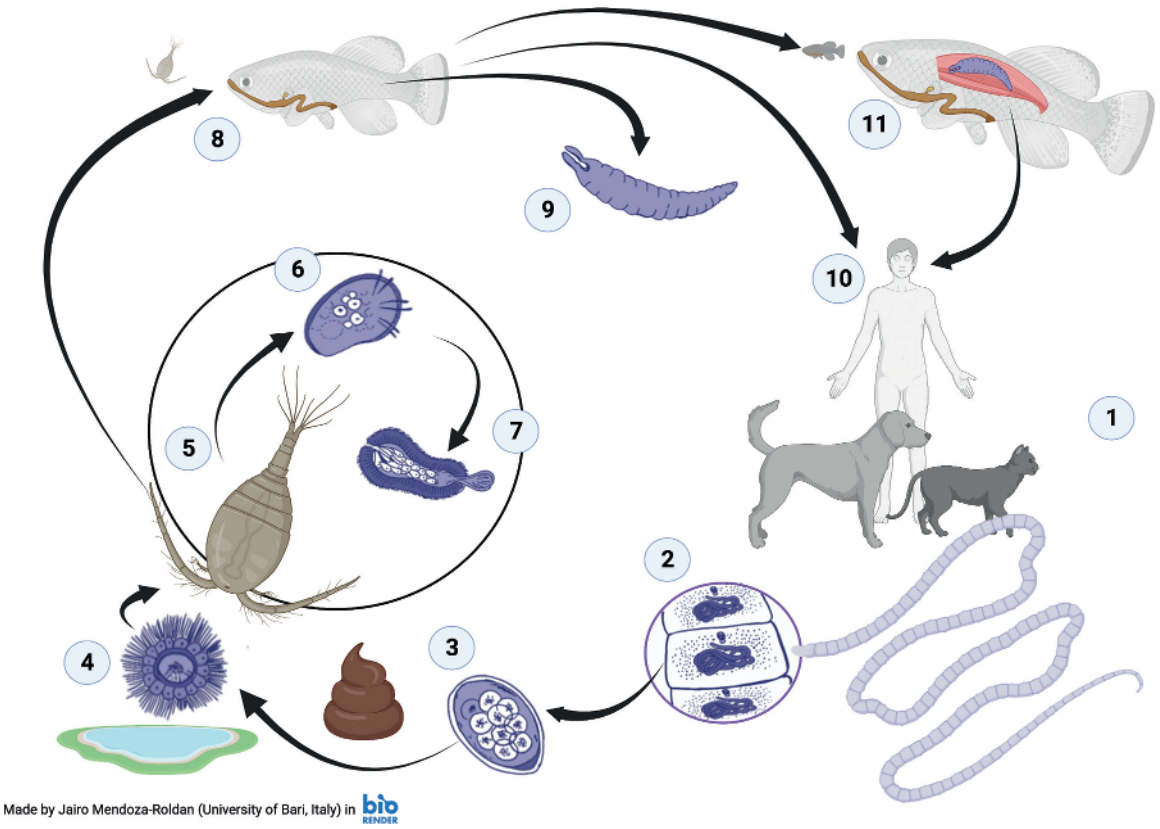
Life cycle: Eggs are continuously discharged from the genital pores of the attached gravid segments of the strobila and pass to the exterior in the faeces. They resemble *F. hepatica* eggs, being

Fig. 1.134 Egg of *Diphyllobothrium latum*.

yellow and operculate, but are approximately half the size (Fig. 1.134). The eggs must develop in water and within a few weeks, each hatches to liberate a motile ciliated coracidium which, if ingested by a copepod, develops into the first parasitic larval stage, a worm-like procercoid. When the copepod is ingested by a freshwater fish, the procercoid migrates to the muscles or viscera to form the second larval stage, the plerocercoid; this solid larval metacestode is about 5 mm long and possesses the characteristic scolex. The life cycle is completed when the infected fish is eaten raw, or insufficiently cooked, by the final host. Development to patency is rapid, occurring within 3–4 weeks of ingestion of the plerocercoid. However, if the infected fish is eaten by a larger fish, the plerocercoid has the ability to establish itself in its new host. See **life cycle 28**.

LIFE CYCLE 28. LIFE CYCLE OF *DIPHYLLOBOTRIUM LATUM*

Adult parasites live in the small intestine of the definitive host (mainly humans and other fish-eating mammals) (1). This long cestode (that may grow to up to 25 m in length) features a chain of large proglottids, each with a central uterus and a lateral opening (tocostoma) from which eggs are released (2). The operculated, non-embryonated eggs are continuously eliminated by the proglottids (3). Once they reach an aquatic environment within the host faeces, the eggs mature and hatch into motile coracidia (4) that, upon ingestion by aquatic copepods (first intermediate hosts, 5) develop and moult (6) to become procercoids (7). When an infected copepod is ingested by freshwater fish (second intermediate host, 8), the procercoids migrate to the muscles or viscera and become plerocercoids (9). The life cycle is complete when raw or undercooked infected fish is ingested by a suitable definitive host (10). In this host, the plerocercoids, already provided with a scolex, develop into adult cestodes. If the second intermediate host (freshwater fish) is ingested by another predatory fish (11), the plerocercoids remain infective in the muscles of the latter, thus allowing completion of the life cycle if this is ingested by a suitable definitive host (1).



Diphyllobothrium latum

Synonym: *Dibothriocephalus latus*

Description: A very long, ivory-coloured tapeworm measuring up to 10–15 m in length or longer, with several hundred, or in some cases a few thousand, proglottids. The scolex is unarmed, with two weak muscular longitudinal grooves or bothria as organs of attachment. Anterior proglottids are broader than long while the mature and gravid segments are rectangular with a central genital pore. The uterus is situated centrally and is rosette-shaped. The mature and gravid segments are rectangular with a central genital pore, being broader than they are long. The reproductive organs are located at the centres of the segments. Eggs are yellowish-light brown, ovoid with rounded poles, operculate and measure around 66–70 by 45–50 µm (Fig. 1.134). Note that eggs of *Spirometra* spp. are very similar but have more pointed poles (Fig. 1.135).

Spirometra

Spirometra are small to medium-sized tapeworms of dogs, cats and wild carnivores and an occasional human zoonosis (sparganosis). A couple of features enable differentiation from the very similar genus *Diphyllobothrium*: the vagina and uterus exit separately onto the ventral surface of the proglottid; and the uterus has a spiral form whereas in *Diphyllobothrium* it has a rosette shape (Table 1.66).

Fig. 1.135 *Spirometra* egg.

Table 1.66 *Spirometra* species.

Species	Hosts	Site	Intermediate hosts
Spirometra mansoni	Dogs, cats, wild carnivores, occasionally humans	Small intestine	Copepods: *Cyclops* spp. (**procercoid**) Amphibians, reptiles, birds (**plerocercoid**)
Spirometra mansonoides (syn. *Diphyllobothrium mansonoides*)	Cats, bobcats, raccoons, occasionally dogs	Small intestine	Crustaceans (**procercoid**) Rats, snakes, mice (**plerocercoid** or **spargana**)
Spirometra erinacei (syn. *Spirometra erinaceieuropaei*)	Cats, dogs, foxes	Small intestine	Crustaceans (**procercoid**) Frogs (**plerocercoid**)

Life cycle: The morphology and life cycle of these tapeworms are similar to those of *D. latum*, the procercoids being found in crustaceans, such as *Cyclops*, and the plerocercoids in a wide variety of hosts. These can also act as paratenic hosts. The plerocercoids can also transfer between intermediate hosts. The prepatent period is around 20–30 days.

Spirometra mansoni

Description: The adult tapeworms are very similar to *Diphyllobothrium*, the scolex being unarmed and possessing two muscular longitudinal slit-like grooves as organs of attachment. Proglottids possess both a uterine and a vaginal pore and the uterus is spiral in shape. The plerocercoids, also called spargana, are white, ribbon-like, crinkled and can measure around 300–400 mm. The operculate eggs have pointed ends and measure on average 65 by 45 µm (Fig. 1.135).

Spirometra mansonoides

Synonym: *Diphyllobothrium mansonoides*

Description: The adult worms are pinkish in color and gravid proglottids have a tightly coiled uterus full of brown eggs.

Spirometra erinacei

Synonym: *Spirometra erinaceieuropaei*

Description: Adult tapeworms can reach 1.5 m in length and possess a finger-like scolex with the bothria fading into the strobila. The proglottids contain a spiral uterus with 2–3 coils and a dumbbell-shaped ovary that is transversely long.